

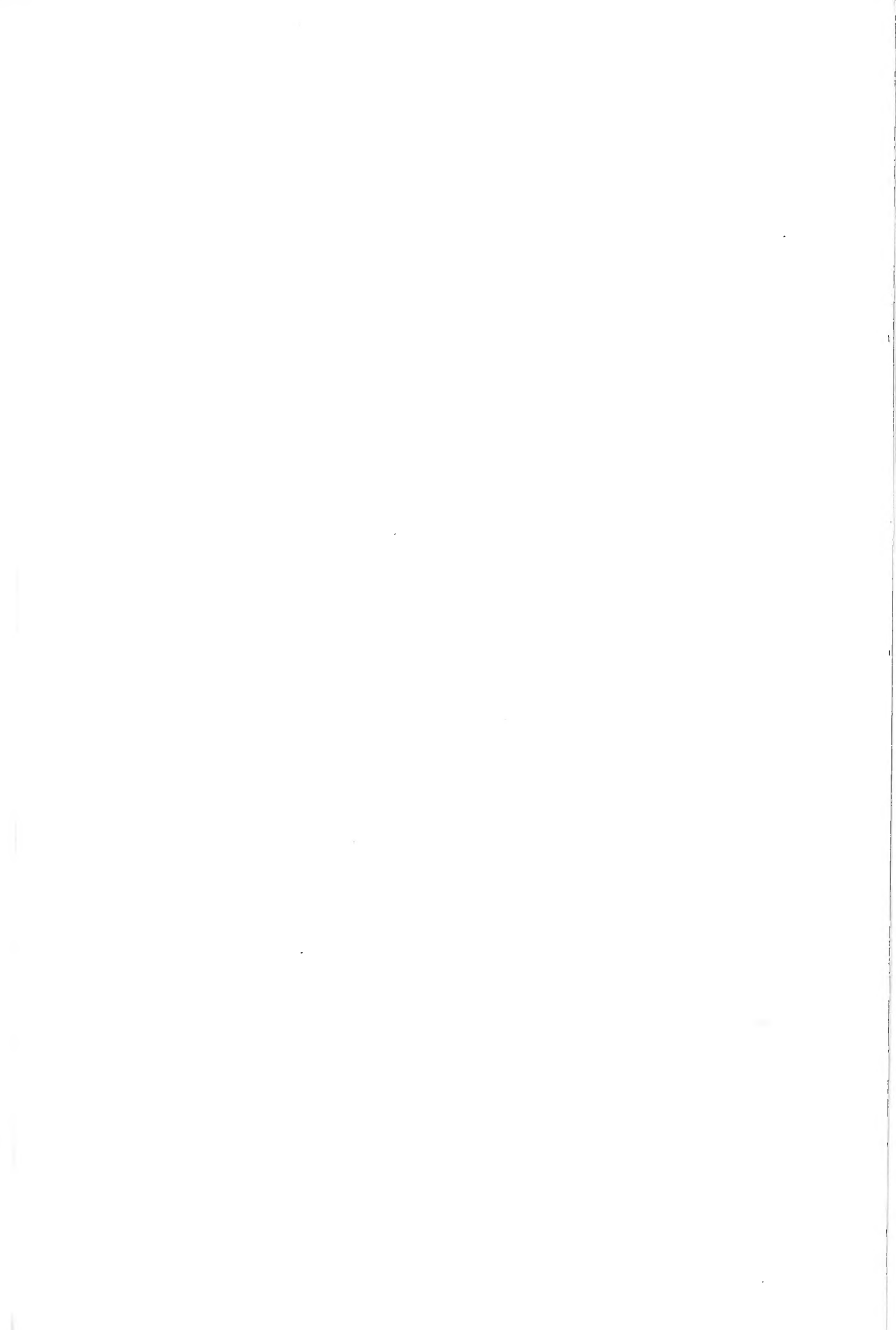


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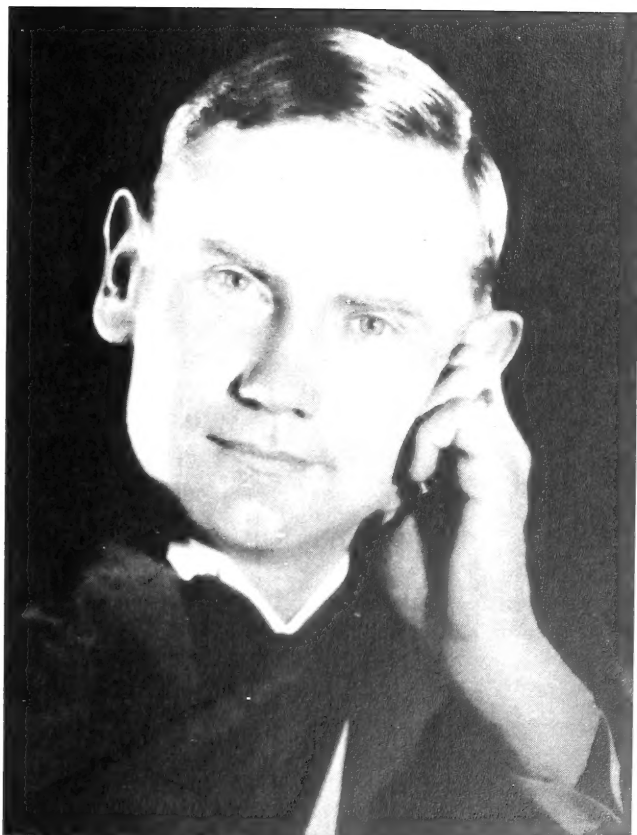
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THIS VOLUME IS DEDICATED TO

JOHN FREDRICK VICARS PHILLIPS (1899—)

D.Sc. (Edin.), F.R.S.E., F.R.S. Afr., F.W.A.

One time Professor of Botany, University of the Witwatersrand, and of Agriculture, University of Ghana. Part-time Consultant in Agriculture and Forestry Development, International Bank of Reconstruction and Development and the Food and Agriculture Organisation. Recently Senior Research Fellow, Co-ordination of Agro-Economic Research (Town and Regional Planning Commission, Natal) in the University of Natal, Pietermaritzburg. President of the South African Association for the Advancement of Science in 1969; Honorary degree (D.Sc.) from Rhodes University, Grahamstown, 1969 and from the University of the Witwatersrand, 1980.

Bio-ecologist and Conservationist, made Frankenwald Estate, (University of the Witwatersrand) a notable centre for ecological research, where the biotic community, climate and edaphic factors, and the impact of fire, grazing and protection of native grassland were studied. His students have held posts in universities and field services from the Cape to the Sudan and the Gold Coast and Australia. His contribution in this way alone speaks for itself. His activities as a member of the Botanical Survey of South Africa led him to make a large botanical survey collection, which is now incorporated in the Moss Herbarium, University of the Witwatersrand.

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: INTRODUCTION AND FORMAT

The *Journal of South African Botany* is instituting a series designed to provide a medium for the publication of data on the karyotypes of Southern African plants. The aim of this series is to provide information not merely on chromosome number, but also on chromosome morphology at as detailed a level as may reasonably be achieved.

Contributions to the series are welcome. There is no prescribed length or order for the articles, but contributors should adhere to the following format:

SCIENTIFIC NAME (including author citation)

CHROMOSOME NUMBER

MATERIAL

METHOD OF PREPARATION

OBSERVATIONS

REFERENCES

The general style of the articles should conform to the first of the series, which is the succeeding article in this volume. In particular, contributors should note the following:

The MATERIAL section should indicate the origin of the material (preferably wild collections) and include a reference to a herbarium specimen deposited in a herbarium of a recognised botanical institution using current *Index Herbariorum* abbreviations. Such specimens should preferably be of the actual plants studied and should be cited under personal collecting numbers where possible.

The METHOD OF PREPARATION should state concisely the technique used. It is strongly recommended that root tip rather than meiotic material be used, as the latter conveys only limited information on chromosome size and morphology.

OBSERVATIONS are always considered useful, but should be concise. Laboratories in which chromosome banding techniques are practised are encouraged to submit banding studies as part of this section.

Articles should include one high quality photograph of the mitotic chromosomes of each of the species considered, on which should be provided a scale lines of 10 μ length. In order to provide an accurate impression of the differences in chromosome size between species, the size at which photographs will be printed will wherever possible correspond to a final magnification of $\times 2\,000$, i.e. with the scale line measuring 20 mm across.

Photographs should be supplemented by an idiogram of the haploid complement, in cases where the size of the chromosomes allows such to be constructed with accuracy. The style of the idiogram should be one in which the centromeres are aligned at the same level. The chromosomes should be arranged in descending order of length, except in the case of nucleolar chromosomes. The latter should preferably be placed at the end of the complement, but in any case where evident should be clearly indicated.

Camera lucida drawings of scattered chromosomes will not be accepted as these convey nothing which cannot better be gained from a good photograph and idiogram.

REFERENCES should wherever possible include previous work on the karyotypes. Journals should be abbreviated according to the *World list of Scientific Periodicals*. References may be combined at the end of an article, if preferable in the interest of brevity.

Those wishing to contribute less detailed cytological data are referred to the parallel series in this journal: *Chromosome Numbers of Southern African Plants*.

CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 1-3.

D. J. MOGFORD

(Department of Plant Sciences, Rhodes University, Grahamstown)

1. *ENCEPHALARTOS LEHMANNII* Ecklon ex Lehm.

CHROMOSOME NUMBER: $2n = 18$ (Figs 1a, b).

ORIGIN OF MATERIAL: Seedling plants from the Grahamstown Botanical Garden. Rhodes University Herbarium accession 24833 (RUH).

METHOD OF PREPARATION: Root tip material. Colchicine pretreatment, Feulgen/Acetic orcein staining.

OBSERVATIONS

The chromosomes adhere to the general scheme for *Encephalartos* described by Marchant (1968), viz. four pairs of metacentric chromosomes and five pairs of submetacentrics, one pair of the latter possessing nucleolar organiser regions. The organiser regions are of a complex beaded appearance, and of a heterochromatic nature as revealed both by allocyclic condensation (Marchant, 1968) and differential fluorescence following denaturation-reannealing treatment (Mogford, 1978, and in press). The chromosomes are large, and the stretching of chromosome arms together with variation in the effectiveness of pretreatment makes accurate size determination difficult.

2. *ENCEPHALARTOS ALTENSTEINII* Lehm.

CHROMOSOME NUMBER: $2n = 18$ (Figs 2a, b).

ORIGIN OF MATERIAL: As in 1. Rhodes University Herbarium accession 24832 (RUH).

METHOD OF PREPARATION: As in 1.

OBSERVATIONS: As in 1.

3. *ENCEPHALARTOS LONGIFOLIUS* (Jacq.) Lehm.

CHROMOSOME NUMBER: $2n = 18$ (Figs 3a, b).

ORIGIN OF MATERIAL: As in 1. Rhodes University Herbarium accession 24834 (RUH).

METHOD OF PREPARATION: As in 1.

OBSERVATIONS: As in 1.

Accepted for publication 18th February, 1980.

1a



FIG. 1A.

E. lehmannii, somatic metaphase. Bar represents 10 μ . Arrows indicate satellites

1b

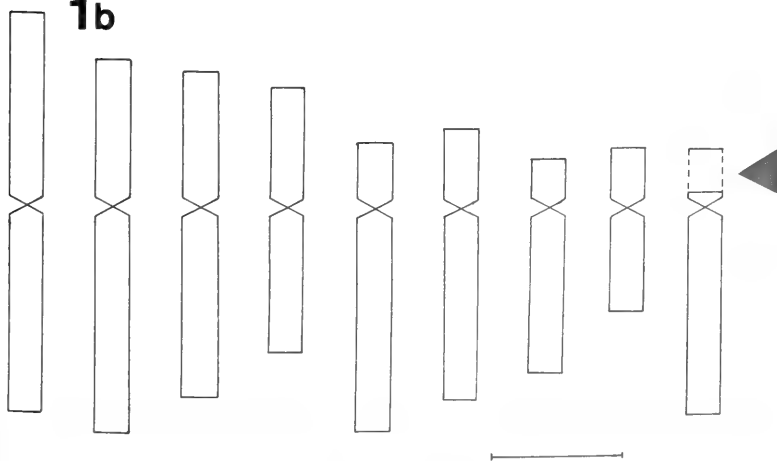


FIG. 1B.

E. lehmannii, haploid chromosome complement. Bar represents 10 μ . Arrow indicates nucleolar organiser region.

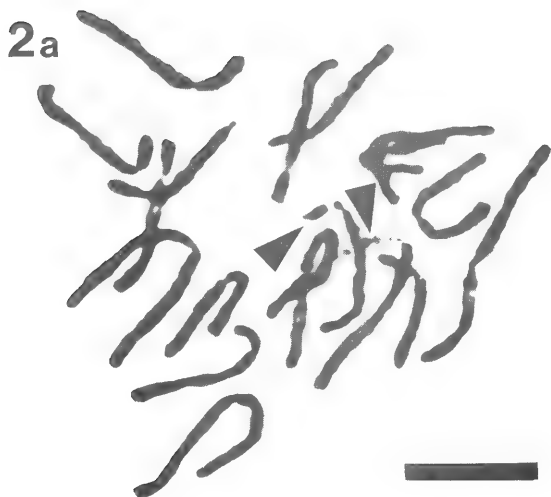


FIG. 2A.

E. altensteinii, somatic metaphase. Bar represents 10 μ . Arrows indicate satellites.

2b

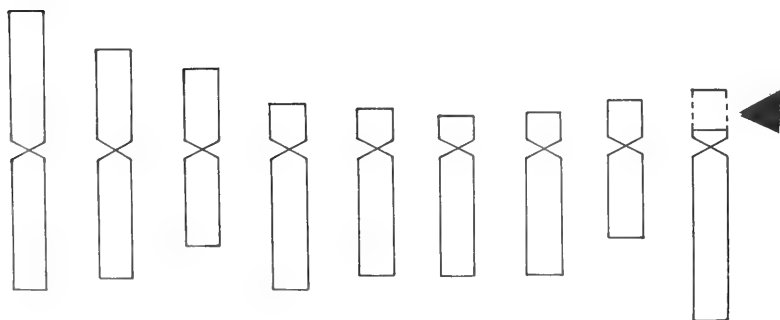


FIG. 2B.

E. altensteinii, haploid chromosome complement. Bar represents 10 μ . Arrow indicates nucleolar organiser region.

3a

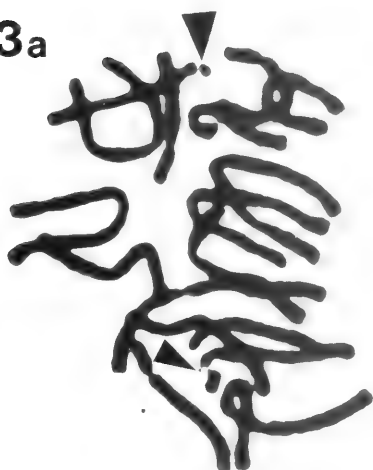


FIG. 3A.

E. longifolius, somatic metaphase. Bar represents 10 μ . Arrows indicate satellites.

3b

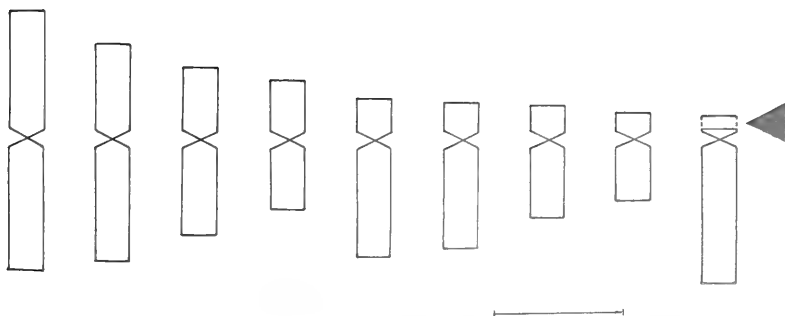


FIG. 3B.

E. longifolius, haploid chromosome complement. Bar represents 10 μ . Arrow indicates nucleolar organiser region.

REFERENCES

- MARCHANT, D. W., 1968. Chromosome patterns and nuclear phenomena in the cycad families *Stangeriaceae* and *Zamiaceae*. *Chromosoma* **24**: 100–134.
- MOGFORD, D. J., 1978. Nucleolar heterochromatin in *Encephalartos*. *Jl S. Afr. Bot.* **44**: 83–87.
- MOGFORD, D. J., 1979. Heterochromatin in *Encephalartos*. *Cytologia* **44**: 951–954.

CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 4-6

C. G. VOSA

(Botany School, South Parks Road, Oxford, England)

D. J. MOGFORD

(Department of Plant Sciences, Rhodes University, Grahamstown)

4. *ALOE COOPERI* Baker

CHROMOSOME NUMBER: $2n = 14$ (Figs 1a, b).

ORIGIN OF MATERIAL: Umzumbe, Natal (Collection C.G. Vosa 411). Fielding-Druce herbarium accession no. 411 C.G.V. (OXF).

METHOD OF PREPARATION: Root tip material. Colchicine pretreatment, Feulgen/Acetic orcein staining.

OBSERVATIONS: A strongly bimodal karyotype, with small terminal satellites on one pair of the larger chromosomes.

5. *ALOE HUMILIS* (L.) Mill.

CHROMOSOME NUMBER: $2n = 14$ (Figs 2a, b).

ORIGIN OF MATERIAL: Hankey, Port Elizabeth (Collection C.G. Vosa 385). Fielding-Druce herbarium accession no. 385 C.G.V. (OXF).

METHOD OF PREPARATION: As in 4.

OBSERVATIONS: In the particular plant examined the largest pair of the smaller chromosomes was heteromorphic.

6. *ALOE VARIEGATA* L.

CHROMOSOME NUMBER: $2n = 14$ (Figs 3a, b).

ORIGIN OF MATERIAL: Oudtshoorn, C.P. Rhodes University herbarium accession no. 24835 (RUH).

METHOD OF PREPARATION: As in 4.

OBSERVATIONS: Small terminal satellites are present on two of the chromosome pairs. The chromosome count agrees with that reported by Snode (1951), but the chromosome morphology differs in that the latter worker reported satellites as being present on only one chromosome pair.

REFERENCES

SNOAD, B., 1951. Chromosome numbers of succulent plants. *Heredity* 5: 279-283.

Accepted for publication 14th March, 1980.

1a

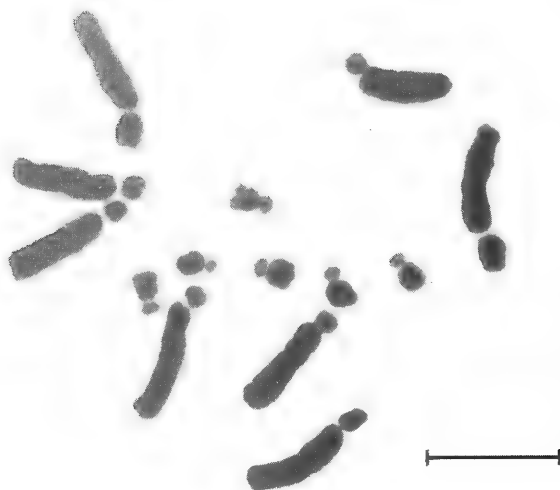


FIG. 1A.

A. cooperi, somatic metaphase. Bar represents 10 μ

1b

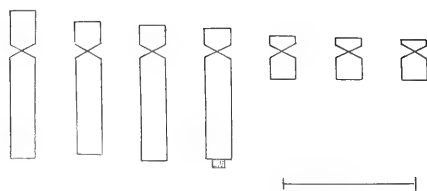


FIG. 1B.

A. cooperi, haploid chromosome complement. Bar represents 10 μ , stippling indicates satellite region.

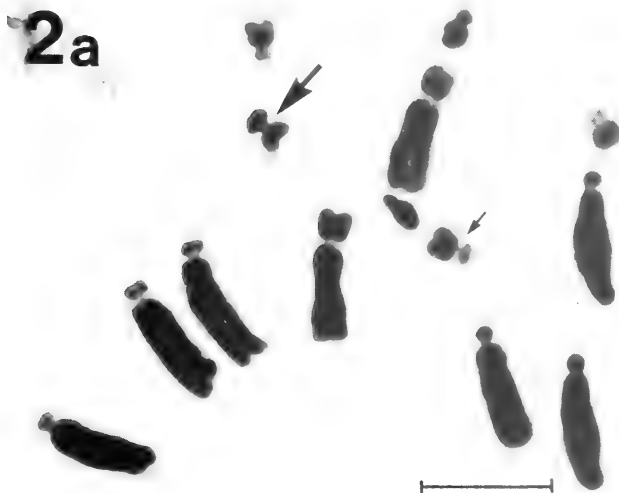


FIG. 2A.

A. humilis, somatic metaphase. Bar represents 10 μ . Large and small arrows represent respectively the normal and variant types of the heteromorphic small chromosome.

2b

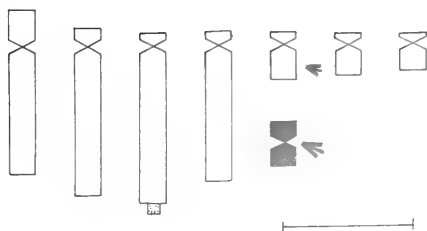


FIG. 2B.

A. humilis, haploid chromosome complement. Bar represents 10 μ , stippling indicates satellite region. Large and small arrows indicate respectively the normal and variant types of the heteromorphic small chromosome.



FIG. 3A.
A. variegata, somatic metaphase. Bar represents 10 μ

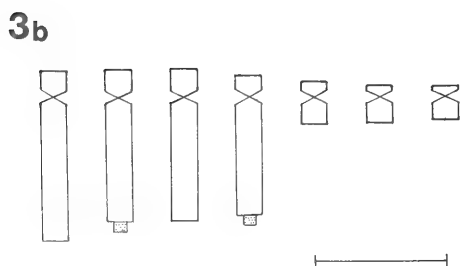


FIG. 3B.
A. variegata, haploid chromosome complement. Bar represents 10 μ , stippling indicates satellite regions.

CHROMOSOME NUMBERS OF SOUTHERN AFRICAN PLANTS: INTRODUCTION AND FORMAT

The *Journal of South African Botany* is instituting a series of reports on chromosome numbers of Southern African plants. This series aims to provide a venue for the publication of miscellaneous chromosome counts which authors have accumulated from time to time and which might not be conveniently accommodated elsewhere. The reports may be of meiotic or mitotic chromosome counts but all numbers should be given as $2n$. No illustration will be accepted.

Format:

Family. Species counted (include author citation).
 $2n = . . .$ Voucher specimen.

Provenance data for voucher specimen should include the following:

Locality where collected in wild, collector's name and collecting number, herbarium where voucher is deposited using *Index Herbariorum* abbreviations.

e.g. ERICACEAE

Erica multumbellifera Berg.

$2n = 36$. Silvermine Plateau, C. A. Smith 3694 (NBG).

Those wishing to contribute more detailed cytological data are referred to the parallel series in this journal: *Chromosome Studies in the Southern African Flora*.

TAXONOMIC STUDIES ON THE *DISINAE*: 1. A REVISION OF THE GENUS *BROWNLEE* LINDL.

H. P. LINDER

(*Bolus Herbarium, University of Cape Town*)

ABSTRACT

The genus *Brownleea* is revised. Six species and two subspecies are recognized. Notes on the taxonomically important morphological characters are given. The habitat of each species is discussed and this is briefly related to the postulated evolutionary patterns in the genus. For each species a full description is given, and the variation, ecology and nomenclature is discussed.

UITTREKSEL

TAKSONOMIESE ONDERSOEK VAN DIE *DISINAE*: 1. 'n HERSIENING VAN DIE GENUS *BROWNLEE* LINDL.

Die genus *Brownleea* word hersien. Ses spesies en twee subspesies word erken. Aantekeninge oor die taksonomies belangrike morfologiese karakters word gegee. Die habitat van elke spesies word beskryf, en word in verband met die moontlike evolusionêre patrone in die genus bespreek. Vir elke spesie word 'n volle beskrywing gegee, en die variasie, ekologie en nomenklatuur word bespreek.

INTRODUCTION

The genus *Brownleea* Lindl. includes six species distributed from Knysna in the southern Cape to Cameroun in the west, northern Kenya in the north and Madagascar in the east. It is a tropical genus, with its centre of diversity in southern Africa. Although the genus is so widely distributed, only one species (*B. parviflora* Lindl.) can be described as being common.

Brownleea was described by Lindley in 1842 from two specimens (*B. parviflora* and *B. coerulea*) collected by the Rev. J. Brownlee. Harvey, to whom Brownlee had sent the material, suggested that the genus (which he rightly thought to be allied to *Disa*) be called after Brownlee (Lindley, 1842). All subsequent authors [with the exception of Reichenbach (1881)], maintained *Brownleea* as a distinct genus allied to *Disa* (Sonder, 1847; Benthams & Hooker, 1883; Pfitzer, 1889; Durand & Schinz, 1894; Kraenzlin, 1900; Schlechter, 1901; Rolfe, 1913; Thonner, 1915; Phillips, 1926; Dyer, 1976). To date a total of 20 names have been proposed in the genus, but no recent critical revision is available. Kraenzlin (1900) and Schlechter (1901) revised the genus when it was still insufficiently known; the majority of the taxa were proposed subsequent to these

Accepted for publication 1st May, 1980.

revisions. Rolfe (1913) dealt only with the South African taxa and did not take sufficient account of the range of variation found in taxa. Summerhayes (1966) critically revised the *Brownleea parviflora* group of species in tropical Africa.

In this study, species are understood to be biological entities (Linder, 1980). In the delimitation of taxa special attention is paid to eco-geographic data. This study is part of a general taxonomic study of the *Disinae*, and the relationships between *Brownleea* and its allies will be discussed in a later paper.

NOTES ON MORPHOLOGY

Tubers

Variation in the hair-covering of the tubers is correlated with the broad habitat type in which the species occurs. The forest taxa have villous tubers, as opposed to the pubescent tubers of the grassland taxa. However, this organ is frequently not collected, so that the data base is insufficient.

Leaves

The number of leaves per plant tends to be constant for each species. However, there are many exceptions and the range of number of leaves found is from one to three, so that this character is of limited use.

Leaf shape is correlated to the broad habitat type. The forest taxa have ovate to narrowly ovate leaves, compared to the narrowly lanceolate to linear leaves of the grassland taxa.

Inflorescence

In inflorescence shape, two directions of development can be traced if the subimbricate to imbricate spike of *B. parviflora* is taken as the starting point. One line leads to the capitate inflorescence of *B. galpinii* s.l., the other leads to the single flowers of *B. macroceras*, via the lax inflorescences of *B. recurvata*, *B. coerulea* and *B. maculata*. The second line is also associated with increase in flower size, and all the correlated changes in floral structure. As floral characters (i.e. the reproductive syndrome) are assumed to be more conservative than vegetative characters (the survival syndrome), inflorescence shape can be taken to reflect phylogenetic relationships.

Sepals

The sepals throughout the genus show little variation in shape, but they provide the best measurable indication of flower size. In *B. parviflora* the sepals do show a more or less square shape; this is interpreted as the effect of reduction in flower size.

Spur

Spur size and shape provides a very important character. Spur length essentially has two states: approximately as long as the dorsal sepal, or more than twice as long as the dorsal sepal. The spur can be sharply decurved, usually near the middle, or it can be gently decurved, or it can be straight. Three combinations of these characters exist in the genus. *B. parviflora*, *B. recurvata* and *B. maculata* have short sharply decurved spurs, *B. galpinii* s.l. has a short straight spur, and *B. macroceras* and *B. coerulea* have long gently decurved spurs.

Petals

Petal size is obviously correlated with sepal size. Petal shape is basically narrowly oblong—lanceolate. From this basic shape the pandurate shape with the upper margins crenulate found in *B. galpinii* ssp. *major* can be derived, via narrowly oblong-pandurate non-crenulate petals of *B. galpinii* ssp. *galpinii*. In *B. parviflora* the petals are oblong to square, possibly the result of reduction in flower size. The development line culminating in *B. macroceras* results essentially in the simplification of the petal into a lorate structure, with the development of anterior basal lobes as in *B. maculata*.

Gynostegium

Apart from size variation, there is no apparent directional development in the various structures of the gynostegium. In *B. parviflora* the whole structure is much reduced, and squat (possibly as a result of the size reduction). In *B. macroceras* with its large flowers, on the other hand, all the structures are slender. In *B. galpinii* s.l. the anther is curved over more than usual in the genus, so that the apex on the anther frequently touches the rostellum. In *B. coerulea* the central lobe of the rostellum is well developed, and almost as tall as the lateral lobes.

Discussion

These morphological data are used to group the taxa into species pairs, and to arrange the species pairs into a natural sequence or a cladogram (Fig. 1). This is the sequence which is compatible with the maximum number of evolutionary sequences for individual morphological characters.

PHYTOGEOGRAPHY, ECOLOGY AND SPECIATION

The genus *Brownleea* occurs in the Afro-montane Region (White, 1978) and the Austro-Afro-alpine Region (Killick, 1978). In these two chorological Regions essentially five vegetation types occur under well-drained to slightly damp conditions. The seven taxa in *Brownleea* occur in these five vegetation types (see Table 1). Only *B. recurvata* and *B. macroceras* transgress into neighbouring

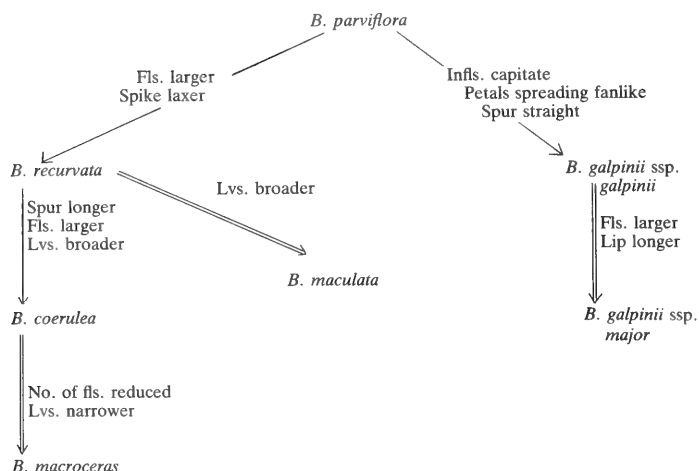


FIG. 1.

Postulated evolutionary relations (cladogram) based on morphological relations. The notes indicate which characters change from one species to the other, the arrows indicate the direction of the change. Single arrows indicate a weak relationship, double arrows a close relationship.

TABLE 1.
Chorological Regions, vegetation types and the species of *Brownleea*.

Chorological Region	Vegetation Type	Species
Austro-afro-alpine	Alpine Belt	<i>B. macroceras</i>
	Subalpine Belt	<i>B. macroceras</i> <i>B. galpinii</i> ssp. <i>major</i>
Afro-montane	Secondary Fynbos	<i>B. recurvata</i>
	Secondary Grassland	<i>B. galpinii</i> ssp. <i>galpinii</i> <i>B. parviflora</i>
	Montane Forest	<i>B. coerulea</i> <i>B. maculata</i>

vegetation types. *B. recurvata*, which generally occurs in the fynbos in areas where the climax is probably montane forest, transgresses at the eastern end of its distribution into secondary montane grassland. *B. macroceras* transgresses at the southern end of its distribution into the fynbos of the subalpine belt (Killick,

1978), which is probably the subclimax of montane forests, whereas the bulk of its distribution range falls in the alpine belt in the high Drakensberg. Both these transgressions occur in the overlap zones with the species from which the transgressing species is presumed to have been derived. In the case of *B. macroceras*, the transgressor shows its maximum amount of population variation in this zone.

The only two species which appear to be sympatric in the same broad vegetation zone are *B. parviflora* and *B. galpinii* s.l. Whether they occur in exactly the same habitat has not been determined. On Mont-aux-Sources, where the two species were collected in close proximity, *B. parviflora* occurred in shallow, well-drained rocky soil, while *B. galpinii* ssp. *major* grew in deeper soil in seasonal seepages (Linder 2074 and Linder 2073 respectively).

On morphological grounds, two very closely related species pairs can be postulated in the genus (*B. macroceras*/*B. coerulea* and *B. recurvata*/*B. maculata*). In both cases, the single most important differential character is the leaf shape. In both cases, one member of the pair inhabits montane forest (*B. coerulea* south of the Limpopo and in Madagascar and *B. maculata* north of the Limpopo), while the other member occurs in full sunlight (*B. recurvata* in the fynbos of the Eastern Cape, and *B. macroceras* under alpine and subalpine conditions in the Eastern Cape and Natal). The two subspecies of the polytypic *B. galpinii* separate environmentally into an alpine group (subspecies *major*) and a montane grassland group (subspecies *galpinii*).

By investigating the eco-geographic differences between closely related species (on morphological evidence, see Fig. 1), the factor(s) that may have caused the differentiation that led to the speciation can be postulated. In all the species pairs in *Brownleea* ecological differences between the taxa appear to be more important than geographic isolation. If geographic isolation were important, populations of the same species that are effectively isolated (such as *B. parviflora* and *B. coerulea*, both with an Africa-Madagascar disjunction) should have differentiated into distinct taxa (i.e. speciated). However, if ecological conditions were important, each taxon should only occur in one habitat type. This is generally found to be the case (Table 1).

The postulated scheme of evolution implies that dispersion must occur relatively easily in this genus. This assumption is borne out by the Afro-Madagascan distribution of two species, and by the extra-ordinary outliers of *B. parviflora* on the Cameroon Mountain and in the north of Kenya, with the northern most part of the continuous distribution being in the south of Tanzania (Fig. 10). Although it is possible that this is a relic distribution, the absence of this species from the highlands of Kenya, as well as the relatively specialized nature (and therefore probably evolutionary recent nature) of the genus, argue that these are new colonizations. It is thus considered possible that the prototype of *B. maculata* could have been derived from *B. recurvata*, although the latter occurs more than 1 000 km to the south.

TAXONOMY

Brownleea Lindl.

Brownleea Harv. ex Lindl. in Hook. Lond. J. Bot. 1: 16 (1842).

Leaves 1–3(–5), scattered on the stem, linear to ovate, usually more or less plicate with emergent veins, nitid; flowers white to mauve; dorsal sepal acute to acuminate, usually lanceolate, 3–13 mm tall, spur horizontal at the base; lateral sepals flat, oblique, narrowly elliptical to oblong, acute, 3–18 mm long; petals erect, fused to the dorsal sepal, more or less oblong to lanceolate or pandurate; lip minute, erect in front of the stigma; rostellum lateral lobes erect, lorate, bearing the viscidia at their apexes; caudicles almost as long as the pollen-masses, anther usually apically upcurved; stigma sessile.

Tubers more or less testicular, pubescent to woolly, up to 50 mm long. *Plants* mostly erect, slender, 50–600 mm tall, scape generally nitid, the base rarely with a sheath of old leaf fibres; basal sheath(s) pale brown, often more or less mucronate, obtuse to acute, up to 150 mm long. *Leaves* 1–3 (–5), scattered on the stem, erect to spreading, linear to ovate, acute to sub-acuminate, the blade up to 220 mm long, usually nitid, more or less plicate, with the veins somewhat prominent. *Inflorescence* a capitate to lax spike; flowers single to numerous, from c. 5 mm to 30 mm in diameter, white to mauve or pale with darker mauve spots; bracts shorter than to much longer than the ovary, acuminate, green, erect. *Dorsal sepal* odd, more or less lanceolate, acuminate, falcate in side view, the apex often reflexed, 3–13 mm long; spur horizontal at the base, then either short and sharply downcurved, or short and straight, or up to 50 mm long, slender and gradually decurved. *Lateral sepals* flat, generally oblique, narrowly elliptical, rarely oblong, acute, 3–18 mm long. *Petals* fused by the backs to the dorsal sepal, oblanceolate to oblong to almost pandurate; occasionally with a basal anticous tooth, the upper margin flat or crenulate, apex acute or rounded. *Lip* minute, erect from a broad short base in front of the stigma, 0.1–2 mm long. *Rostellum* tall, erect; lateral lobes more or less lorate, concave, bearing the viscidia at their apexes, central lobe a small fleshy body at the base of the lateral lobes, except in *B. coerulea*, where it is finger-like; staminodes up to as large as the lateral lobes. *Anther* horizontal, the apex generally upcurved, caudicles almost as long as the 2 pollen-masses; viscidia two, globular, separate. Stigma sessile at the base of the rostellum.

Lindley described the genus in 1842 from two species (*B. parviflora* and *B. coerulea*), but failed to select one as the type of the genus. The holotypes of both species are still extant in the Lindleyan herbarium at Kew. *B. parviflora* Lindl. is here selected as the lectotype of the genus.

Lectotype: Brownleea parviflora Lindl.

KEY TO THE SPECIES

1. Flowers in an apical head, or at least strongly apically congested, petals expanded apically, margins crenulate, patent.

- 2. Lateral sepals 6–7 mm long, lip less than 1,5 mm long 6a. *galpinii* ssp. *galpinii*
- 2'. Lateral sepals (6,5–)8–10 mm long, lip more than 1,7 mm long 6b. *galpinii* ssp. *major*
- 1'. Flowers in a lax to subimbricate spike, petals not apically expanded, not patent, margins not crenulate.
- 3. Spur more than twice as long as the dorsal sepal, straight or gradually decurved.
 - 4. Leaves 1(–3), narrowly lanceolate, less than 10 mm wide, plants with 1–3 (–5) flowers 1. *macroceras*
 - 4'. Leaves 3, lanceolate, wider than 10 mm, plants with (5–)6–15 flowers 2. *coerulea*
- 3'. Spur less than twice as long as the dorsal sepal, sharply and geniculate-decurved.
 - 5. Dorsal sepal less than 6 mm long, flowers in dense to rarely lax many-flowered cylindrical spikes 5. *parviflora*
 - 5'. Dorsal sepal more than 5 mm long, flowers in lax several-flowered spikes.
 - 6. Leaves linear to narrowly lanceolate, width less than 10 mm 3. *recurvata*
 - 6'. Leaves lanceolate to narrowly ovate, width more than 10 mm 4. *maculata*

1. *Brownleea macroceras* Sond. in *Linnaea* **19**: 106 (1847). Type: Eastern Cape, Stockenstrom Division, Katriviersberg, 5 000 to 6 000 feet, above forest, March, Ecklon and Zeyher s.n. (S!, holotype; K!, W!).

Disa macroceras (Sond.) Reichb.f., *Otia Bot.* Hamb. **2**: 119 (1881).

Brownleea monophyllum Schltr. in *Bot. Jahrb.* **31**: 307 (1901). Type: Grassland on the summit of Drakensberg, altitude 9 000 to 10 000 feet, Feb. 1893, Thode 52 (B†, holotype; K!).

Brownleea coerulea sensu Bolus in *J. Linn. Soc.* **25**: 204 (1889) as to *B. macroceras*.

Icon: *Fl. Pl. S. Afr.* **19**: t.740 (1939).

Flowers large (lateral sepal (10–)13–18 mm long), spurs long [(15–)25–40 mm], 1(–6) flowers per inflorescence and with 1(–3) narrowly lanceolate leaves.

Tubers c. 15 mm in diameter. *Plants* erect or upcurved, (50–)100–300(–500) mm tall; basal sheath hyaline to pale brown, obtuse and apiculate, ribbed and with dark-brown muricate patches, (20–)40–80 mm long. *Leaves* 1(–3), scattered on the scape, shortly sheathing at the base, the blade usually narrowly lanceolate, acute to very acute, spreading, shallowly conduplicate, 60–80(–120) mm long and 4–10(–30) mm wide. *Inflorescence* 1(–6) flowered; ovary slender, up to 25 mm long; bracts up to 8 mm wide at the base, acuminate, as long as or shorter than the ovary, the midvein prominent; flowers up to 30 mm in diameter, facing out horizontally; lateral sepals and petals pale mauve to almost white, dorsal sepal muddy mauve, apex of the spur purplish or green, base of the petals purple, rostellum white and stigma blue-mauve. *Dorsal sepal* galeate, narrowly oblong to lorate or lanceolate, laterally flattened, the apex reflexed, galea 10–13 mm tall, c. 2–3 mm wide and 3–6 mm deep; spur slender cylindrical, from a short conical base, horizontal at the base and at length somewhat decurved, apically subclavate, obtuse; (15–)25–40 mm long. *Lateral sepals* oblique, narrowly elliptical, acute, flat, spreading forwards and down. (10–)

13–18 mm long and 4–6 mm wide. *Petals* oblanceolate to narrowly obovate, suboblique, acute, facing forwards, 10–14 mm long and 4–5 mm wide. *Lip* linear, ascending in front of the stigma, c. 2 mm long. *Rostellum* erect, 3–5 mm tall, lateral lobes well developed, shallowly concave, staminodes c. 1 mm in diameter; anther c. 3 mm long, the apex upcurved, viscidia spherical; stigma c. 2,5 mm in diameter, sessile at the base of the rostellum. (Fig. 2).

B. macroceras was described by Sonder in 1847 from material collected by Ecklon and Zeyher from near the southern end of the distribution range of this species, on the Katriviersberg. The specimens are 2(–3) leaved, and the flowers are somewhat smaller than average. Bolus (1889, 1896), Kraenzlin (1900) and Schlechter (1901) included *B. macroceras* in *B. coerulea* Lindl. No reasons are given, but as will be shown below, ignorance of the morphological and ecological ranges of *B. macroceras* and *B. coerulea* probably caused this confusion.

In 1901 Schlechter described *B. monophyllum*. He cites as type a Thode specimen, collected from the Drakensberg. This was probably from the Montaux-Sources area, where Thode is known to have collected (Killick, 1977). Schlechter compared the new species to *B. coerulea* and *B. madagascarica*, to which it is doubtlessly allied. He considered that the single leaf found on the type specimen is an important differential character: “a character, that should not be underestimated in *Brownleea*”. However, field studies have shown that this character is variable in natural populations. Schlechter’s treatment was followed by Rolfe (1913), Bolus (1939) and Jacot Guillarmod (1971). Bolus (1939) noted that: “Probably, when ample living material is available for study, the two species (*B. monophyllum* and *B. macroceras*) will prove to be identical”.

VARIATION

A geographic gradient can be detected in the variation patterns. In the northern part of the distribution range, the plants tend to be smaller, more frequently single-flowered with a single leaf. The flowers also tend to be larger. In the Katberg (southern end of the distribution), individuals with up to 6 flowers and 3 leaves occasionally occur, but the flowers tend to be smaller. Within populations, the range of variation also increases from the north to the south, and populations on the Katberg (*Linder 2111*) range in size from 400 mm tall (in wet shaded seepage conditions) to less than 100 mm tall on dry ledges with shallow soils.

ECOLOGY AND PHYTOGEOGRAPHY

B. macroceras is distributed from Harrismith in the Orange Free State, along the Drakensberg to the Winterberg (Queenstown Division) in the Eastern Cape. In the north it occurs above 2 700 m, and in the south above 1 800 m. Throughout its range it is generally associated with rock outcrops, where it occurs on rock ledges and in shallow rocky soil.

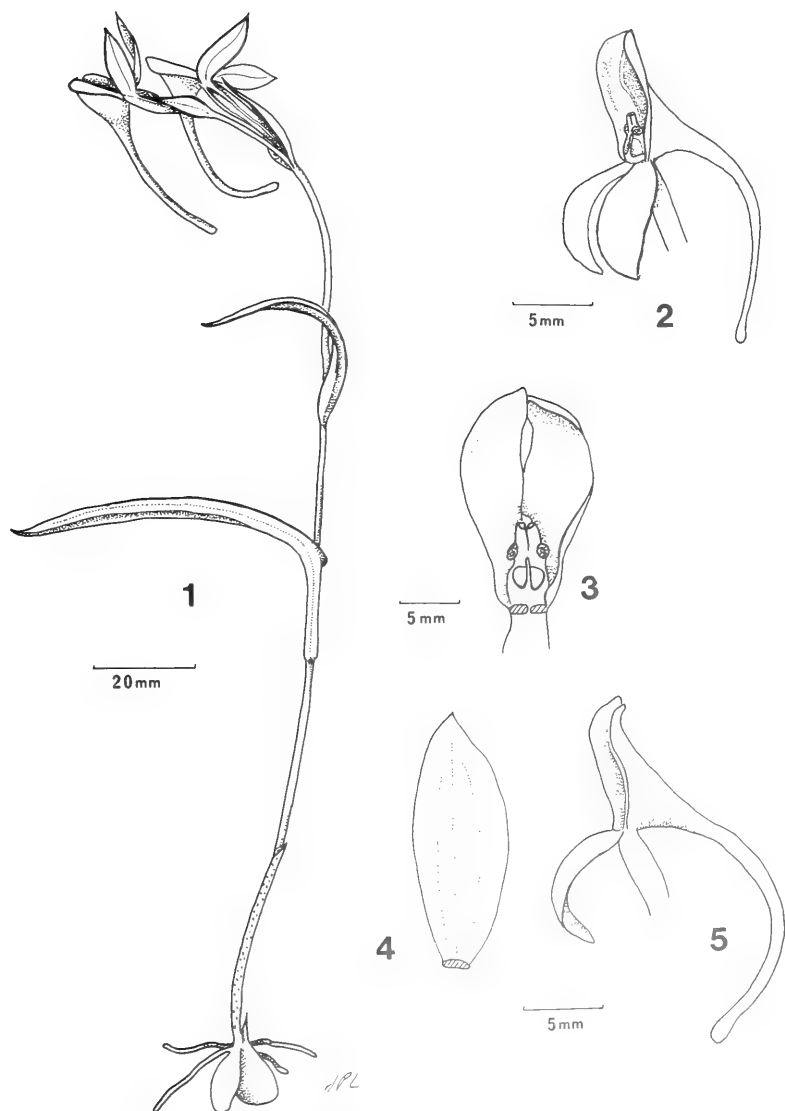


FIG. 2.

B. macroceras. 1. Whole plant (Linder 2075). 2-5. Floral structure (Linder 949): 2. Side view of flower; 3. Column, petals and lip; 4. Lateral sepal; 5. Spur and dorsal sepal.

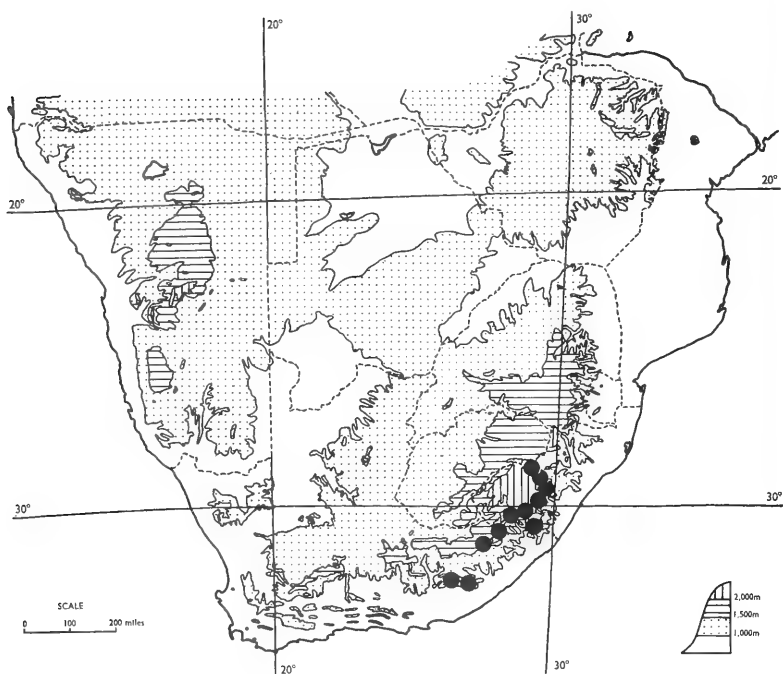


FIG. 3.
Distribution of *B. macroceras*.

In the Drakensberg *B. macroceras* occurs in the alpine belt, in *Danthonia*–*Festuca*–*Pentstemon* grassland (Killick, 1963; West, 1951). In the Eastern Cape it grows in depauperate macchia (Story, 1951). In the Drakensberg this species is associated with basalt rock or derived soils, while in the Eastern Cape it is associated with dolerite. The climate throughout the area is severe, with snow in winter, and frequent mist in summer. In the north almost all rain falls in summer, but in the Eastern Cape up to 30 % of the rain falls in winter (Story, 1951). Recorded rainfall in the Drakensberg is 1 609 mm p.a. at the Organ Pipes Pass (Cathedral Peaks Area) (Killick, 1963) and 1 271 mm p.a. in the Mont-aux-Sources area at c. 3000 m (Herbst & Roberts, 1974). In the Hogsback area rainfall is about 1 100 mm p.a. (Story, 1951).

This appears to be the only species that is scented.

Generally the plants are common in suitable habitats, but dense populations

are not formed. Flowering occurs from late February until the beginning of April.

REPRESENTATIVE COLLECTIONS

Lesotho, between Indumeni Dome and Castle Buttress, frequent in alpine grassland, flowers light purple, 6.II.1949, *Killick 2319* (PRE, BM, K); Eastern Cape, Maclear, ascent to Naudés Nek, c. 2 500 m, wet scree slopes, flowers white to deep lilac, 19.II.1971, *Hilliard & Burt* (NU, K); Eastern Cape, King William's Town, Gaikas Kop, 1 800 m, very common in moist mossy cracks in cliffs, flowers very pale mauve to almost white, 14.II.1977, *Linder 1055* (BOL).

2. *Brownleea coerulea* Harv. ex Lindl. in Hook. Lond. J. Bot. 1: 16 (1842). Type: Eastern Cape Province, near King William's Town, among trees, March 1841, *Brownlee s.n.* (K!, holotype).

Disa coerulea (Harv. ex Lindl.) Reichb.f., Otia Bot. Hamb. 2: 119 (1881).

Brownleea madagascariensis Ridley in J. Linn. Soc. 22: 126 (1885). Type: Madagascar, Imerina, *Fox s.n.* (K!, holotype).

Brownleea nelsonii Rolfe in Fl. Cap. 5, 3:262 (1913). Type: Transvaal, *Nelson 16* (K!, holotype).

Brownleea woodii Rolfe in Fl. Cap. 5, 3: 262 (1913). Syntypes: Natal, in stony bush near Murchison, 2 000 feet, *Wood 1982, 3179* (K!, syntypes).

Icones: Curtis's Bot. Mag. t.7309 (1893). H. Bolus, Icones Orch. Austro-Afr. 1: t.40 (1896). Fl. Pl. S. Afr. 18: t.702 (1938).

Flowers large (lateral sepal 8–12 mm long); spur long, slender (13–26 mm long); inflorescence subimbricate 3–15–30-flowered; leaf narrowly ovate to rarely narrowly lanceolate (wider than 10 mm).

Tubers usually woolly, spreading, 15–40 mm long, 10–20 mm in diameter. *Plants* erect, 100–350–600 mm tall, basal sheaths usually two, the outer often, and occasionally both, lost, generally obtuse, apiculate, the inner up to 140 mm long, the veins emergent and the surface muricate. *Leaves* (2–)3(–4), scattered on the scape, shortly sheathing at the base, the blade spreading, narrowly ovate, rarely narrowly lanceolate, subacuminate, subcordate at the base, up to 220 mm long and (15–)40(–65) mm wide, the central vein somewhat emergent below. Inflorescence subimbricate, oblong, 30–60–100 mm long and 3–15–30-flowered; ovary 10–20 mm long, generally the longest near the base of the inflorescence; bracts narrowly lanceolate, very acute to acuminate, overtopping the flowers at the base of the inflorescence, shorter than the ovaries near the apex; flowers c. 20 mm in diameter, spreading horizontally, mauve, often with deep purple dots on the galea. *Dorsal sepal* galeate, lanceolate in front view, falcate in side view, acuminate, 8–8.5–10 mm long, galea c. 3 mm deep and 1 mm wide; spur slender cylindrical from a shortly conical base, horizontal at the base, the apex subclavate, frequently decurved, spur 13–20–26 mm long. *Lateral sepals* oblique, nar-

rowly elliptical, acute to subacute, spreading with the inner margins parallel, 8–9.5–13 mm long. *Petals* narrowly oblong from a slender basal limb, apically more or less truncate, the rear base of the blade toothed, petal more or less as long as the dorsal sepal, the blade frequently conduplicate, the basal limb attached to the rostellum. *Lip* minute, linear, erect in front of the stigma, c. 1 mm long. *Rostellum* angled backwards, c. 2 mm tall, lateral lobes shallowly grooved, truncate, central lobe finger-like, as tall as the lateral lobes, acute, staminodes c. 1 mm in diameter, pearly; anther c. 2 mm long, strongly up-curved; stigma vertical on the base of the rostellum.

Brownleea coerulea has generally been recognized as a distinct species. Bolus (1889) included *B. macroceras* Sond. in *B. coerulea*, and was followed by Kraenzlin (1900) and Schlechter (1901).

Brownleea madagascariensis was described by Ridley, who noted its similarity to *B. coerulea*. As a differentiating character he mentions that the petals are fused to the galea by their backs, and not by the inner margins as would be expected, but this is characteristic for the whole genus, a fact Ridley seems to have been unaware of. Kraenzlin (1900) and Schlechter (1901) maintained it as a distinct species, although Schlechter remarked that only the remarkable geographic distribution and some (undefined) differences in the galea separated it from *B. coerulea*.

Both *B. nelsonii* and *B. woodii* were separated from *B. coerulea* on leaf width. The two syntypes of *B. woodii* were collected on the same day (30.IV.1884) at Murchison—they could be the same collection. Rolfe stated that it is "Distinguished from *B. coerulea* Harv. by its narrower leaves and smaller, differently coloured flowers". The leaf width falls at the lower extreme of the range recorded in the species, but flower size and colour do not appear to be exceptional. There appears to be even less difference between *B. nelsonii* and *B. coerulea*. Flower structure is identical. The leaves of the type are folded, making measurement difficult, yet Rolfe uses leaf width as the key character to separate this species from *B. coerulea*.

VARIATION

The variation in leaf width follows geographical patterns (Fig. 4). Collections from the Eastern Cape tend to have broader leaves (35–60 mm wide) than collections from Natal (25–45 mm wide). Collections from the Transvaal straddle the whole range. Not enough material is available for a statistical analysis.

ECOLOGY AND PHYTOGEOGRAPHY

B. coerulea has a remarkable disjunct distribution: in South Africa it is distributed from King William's Town in the south along the montane or sub-montane forest belt to Pilgrims Rest in the Eastern Transvaal, and it also occurs on the

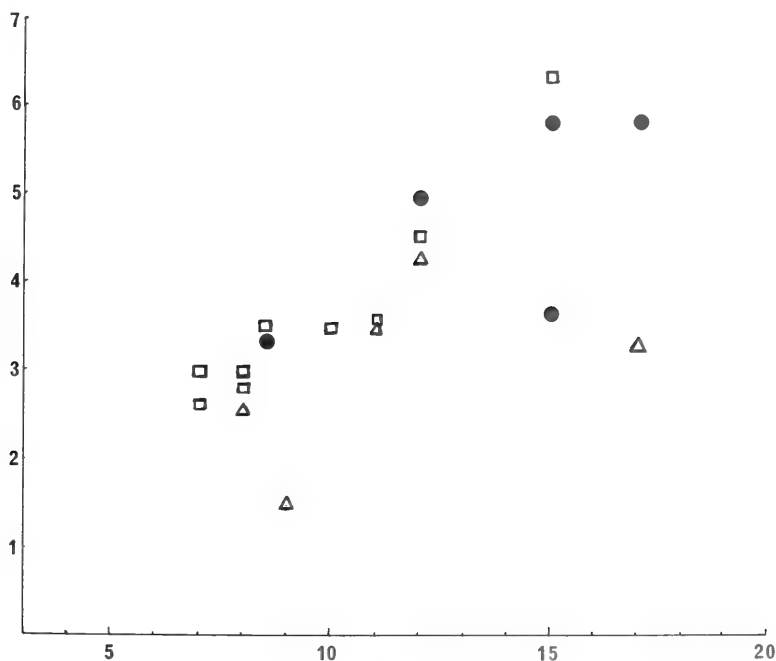


FIG. 4.

Variation in the leaf width of *B. coerulea*. ● = Eastern Cape; △ = Natal; □ = Transvaal and Swaziland.

central mountains of Madagascar. Throughout its range this species occurs in shaded habitats, usually in forests or forest patches, growing on old tree trunks, in moss, and on rock ledges.

The climate over its distribution range is temperate to sub-tropical. Rainfall over the whole area is above 1 000 mm p.a. (W.B. 20; Jackson, 1961), and most of the rain falls in the summer months. Snow does not occur (Koechlin, 1972).

The altitudinal range of this species in the north (Pilgrims Rest) is from 1 000 to 1 500 m, whereas in the south the species occurs at sea-level. Flowering time is from February to April, but in Madagascar the flowering season is somewhat later, from March to June.

REPRESENTATIVE COLLECTIONS

Swaziland, Mbabane, Dalriach Plantation 1 350 m. 5.III.1957, *Compta* 26730 (PRE, NBG); Natal, Port Shepstone, Izotsha Falls, in shade of vegetation

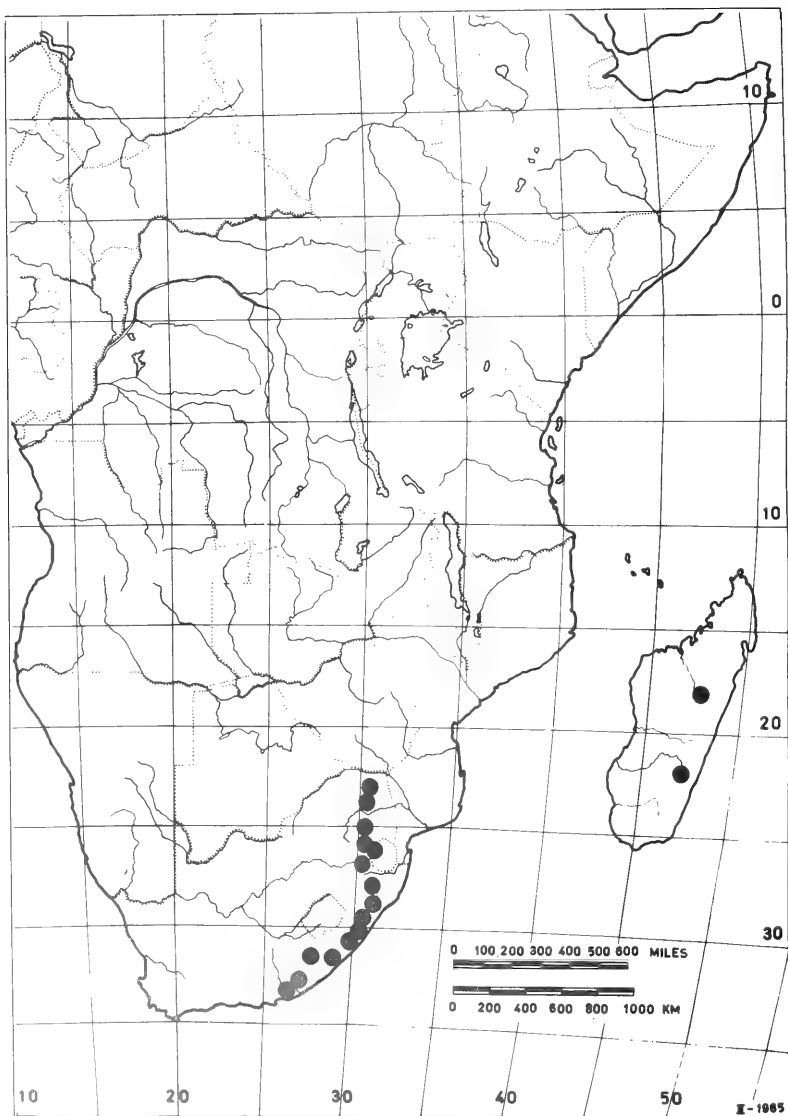


FIG. 5.
Distribution of *Brownleea coerulea*.

at edge of falls, 22.II.1964, *Hilliard 2749* (NU); Transvaal, Barberton, Ngomangoma Falls, shaded ledges, flowers purple lilac with black spots on the hood, 1.IV.1975, *Stirton 1762* (PRE); Eastern Cape, Pirie Forest, damp shady places, 1 000–1 200 m, IV.1888, *Scott-Elliot 913* (BM, K); Madagascar, Ambatoway, near Tananarive, woodland, IV.1957, *Bosser 11085* (P).

3. ***Brownleea recurvata*** Sond. in *Linnaea* 19: 107 (1847). Type: Eastern Cape Province, Uitenhage, along Elandsriver, March, *Ecklon & Zeyher s.n.* (S!, holotype; W!).

Disa recurvata (Sond.) Reichb.f., *Otia Bot. Hamb.* 2: 119 (1881).

Brownleea natalensis Rolfe in *Fl. Cap.* 5, 3: 262 (1913). Type: Natal, near Byrne, *Wood 3177* (K!, holotype).

Icones: Bolus, *Icones Orch. Austro-Afr.* 1: t.41 (1896). Harvey, *Thes. Cap.* 2:t.104 (1863).

Flowers medium-sized (lateral sepal 8–11 mm long); spur sharply decurved, 5–10 mm long; inflorescence a lax spike; leaves linear to narrowly lanceolate, 8(–14) mm long.

Tubers hirsute, 10–30 mm long and 5–10 mm in diameter. *Plant* erect, occasionally subflexuose, (200–)400(–500) mm tall; basal sheaths two, the outer obtuse, 20–40 mm long, often lost; the inner up to 100 mm long, acuminate; both sheaths with prominent veins, often muricate. *Leaves* 2(–3), scattered on the scape, shortly sheathing at the base, the lower leaf the largest, up to 200 mm long and 8(–14) mm wide, linear, lanceolate, very acute to acuminate, erect, veins prominent below. *Inflorescence* lax, up to 150 mm long, (3–)12–17-flowered; ovary 10–15 mm long; bracts lanceolate, acuminate, usually slightly overtopping the flowers; 15–25 mm long, the lower bracts longer than the upper; flowers c. 10 mm in diameter, horizontal, white to soft pink, with a couple of red-brown-purple spots on the upper petal lobe, spur darker pink than the flowers. *Dorsal sepal* galeate, lanceolate, falcate in side view, acuminate, the apex occasionally reflexed, 7–8, 7–12 mm long, galea c. 3 mm wide and 3 mm deep; spur cylindrical occasionally somewhat clavate, horizontal at the base and usually decurved from the middle, 5–7, 3–10 mm long. *Lateral sepals* sub-oblique, narrowly elliptical, very acute, spreading forwards, 8–8, 9–11 mm long. *Petals* suboblique, narrowly oblong, somewhat shorter than the dorsal sepal, somewhat broader towards the base, a small basal anticus lobe flanking the stigma. *Lip* linear, c. 1 mm long, erect in front of the stigma. *Rostellum* erect, c. 3 mm tall, lateral lobes lorate, truncate, concave, staminodes c. 1 mm tall, almost reaching the tip of the lateral lobes; anther c. 3 mm long, the apex upcurved; stigma vertical, sessile at the base of the rostellum. (Fig. 6).

B. recurvata has been recognized as a distinct taxon by all authors that have dealt with this genus.

Rolfe did not indicate why he separated *B. natalensis*, nor to which species it

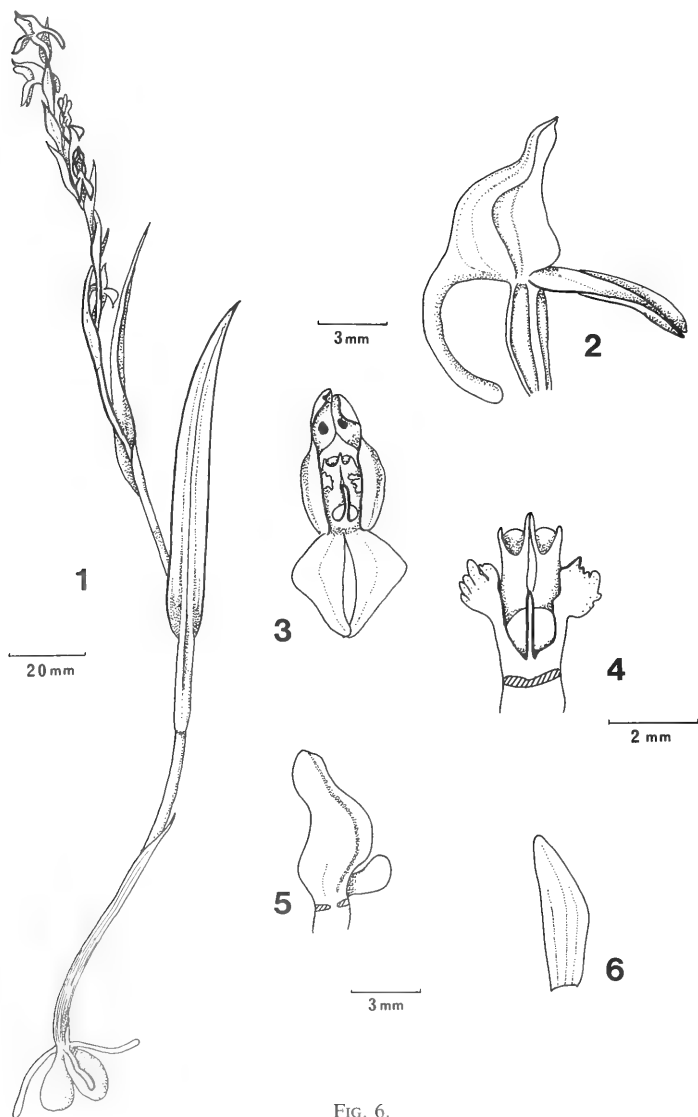


FIG. 6.

B. recurvata. 1. Whole plant (Linder 2094). 2–6. Floral structure (Batten); 2. Side view of flowers; 3. Front view of flower; 4. Rostellum structure; 5. Petal structure; 6. Lateral sepal in two dimensions.

was allied. He placed it near *B. recurvata*, from which he separated it in his key by the spotted flowers and the crenate petals. Investigation of the type specimen revealed that the spots are probably necrotic (this is apart from the spots normally found in this species on the petals). The petals are not markedly crenate—certainly not sufficiently to warrant specific distinction.

ECOLOGY AND PHYTOGEOGRAPHY

B. recurvata extends from Knysna in the Southern Cape Province to East Griqualand. In this area it occurs in well-drained localities, often in pebbly soils, or rarely in damp localities. In the south it is associated with fynbos vegetation and in East Griqualand it has been collected in *Themeda triandra* grassland. In general it occurs below 1 500 m altitude.

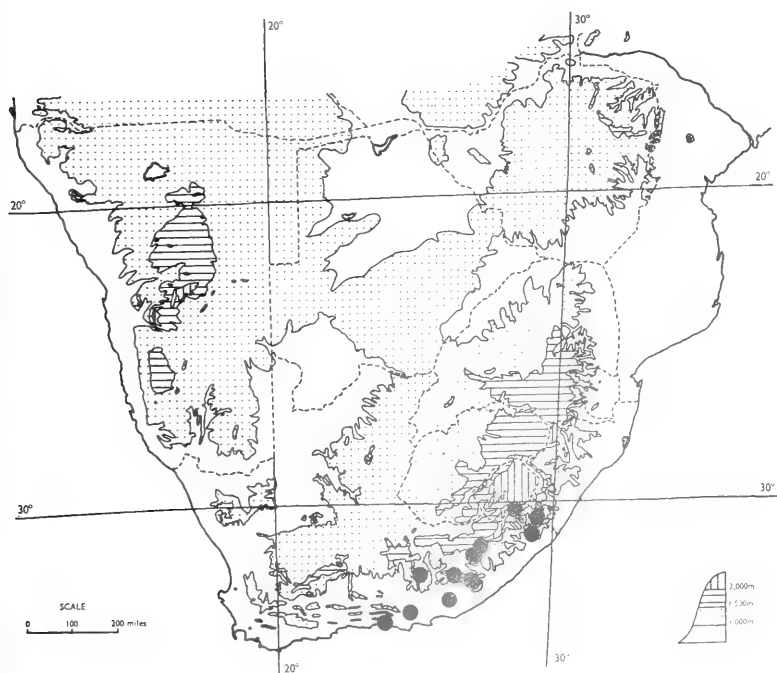


FIG. 7.
Distribution of *B. recurvata*.

Although the climate over the whole distribution range is fairly temperate, it changes from an all-year rainfall regime in the south to a summer rainfall regime in the north-east. In the Knysna area rainfall is about 1 100 mm p.a., fairly evenly distributed over the whole year (W.B. 20, 35). Over the rest of the distribution range the rainfall is about 700 mm p.a., concentrated in the summer months. In East Griqualand 70 % of the rain falls between November and April.

Populations tend to be scattered in suitable habitats, and no dense stands of this species have been seen. Flowering occurs from the end of February to the beginning of April.

REPRESENTATIVE COLLECTIONS

Eastern Cape, mountain slopes above Grahamstown, III.1892, *Glass* in *MacOwan & Bolus 1377* (BOL, BM, K, SAM, ZT, P, G, UPS, W); Transkei, Tabankulu, steep rocky grassy hillside, flowers white to very pale pink, spotted purple inside the hood, 16.II.1971, *Hilliard & Burt 6508* (NU, PRE, K); Southern Cape Province, Tzitzikamma, Ratels Bosch Flats, 180 m, *Fourcade 554* (BOL).

4. ***Brownleea maculata*** Cribb in Kew Bull. 32: 147 (1977). Type: Zimbabwe, Chimanimani Mountains, 6.VI.1949, *Wild 2913* (K!, holotype; SRGH!).

Icon: Kew Bull. 32: 148 (1977).

Flowers medium-sized (lateral sepals 6–7 mm long); spur decurved in the middle, 6–8 mm long; inflorescence a severally flowered lax spike; leaves lanceolate to narrowly ovate.

Tubers c. 35 mm long and 15 mm in diameter, densely villous, not well known. *Plant* 150–350 mm tall, often somewhat flexuose; basal sheath fibrous, acute, up to 100 mm long, frequently lost. Leaves (2–)3, lanceolate to narrowly ovate, acute to acuminate, shortly sheathing at the base, the blade somewhat ascending, up to 110 mm long and 40 mm wide, the veins emergent. *Inflorescence* lax to subimbricate, several to many-flowered, up to 100 mm long; ovary slender, 10–15 mm long; bracts lanceolate to narrowly lanceolate, acuminate, the lowest bract frequently leaf-like, up to 45 mm long, the remainder usually less than 20 mm long; flowers c. 8 mm in diameter, horizontal, sepal mauve-purple, petals white, laterals and petals purple-spotted and striped. *Dorsal sepal* galeate; galea narrowly ovate, acute, falcate in side view, 6–7 mm tall, 2.5 mm wide and 1.5–2 mm deep; spur cylindrical from a short conical base, soon sharply decurved to recurved, apex subclavate, rounded, 6–8 mm long and 0.8 mm in diameter. *Lateral sepals* oblique, narrowly elliptical, acute, spreading forwards, flat, 6–7 mm long and 2–3 mm wide. *Petals* erect, obovate, subacute, with a large basal anticus tooth flanking the stigma, c. 6 mm long and 1.5–2 mm wide. *Lip* minute, erect, c. 2.8 mm long and 0.5 mm wide. *Rostellum* c. 2.5 mm tall, lateral lobes tall, concave, staminodes large; anther c. 2 mm long, sharply up-curved from a horizontal base; stigma vertical.

ECOLOGY AND PHYTOGEOGRAPHY

B. maculata occurs in forests and shaded conditions in the Eastern Highlands of Zimbabwe and on Mt. Mlanje in Malawi. It has not been recorded from altitudes below 1 500 m. The most common substrate is old rotting tree-trunks, although one collection has been made from quartzite rock in deep shade. It occurs both in *Philippia* woodland, as well as other types of woodland (i.e. *Wid-dringtonia* forest on Mt. Mlanje).

The climate is generally equitable, almost temperate, and temperature extremes are not severe. Rainfall on Mt. Mlanje ranges from 1 710 mm p.a. to 2 934 mm p.a. (Chapman, 1962), and in Zimbabwe the rainfall is c. 1 400 mm p.a. (Jackson, 1961).

The flowering time is from March to June, with one record from Mt. Mlanje from August.

REPRESENTATIVE COLLECTIONS

Malawi, Mt. Mlanje, Sumbani Plateau, 2 000 m, shade of *Philippia* near stream, flowers purple with darker spots, 12.V.1963, *Wild* 6230 (BOL, SRGH, K); Zimbabwe, Chimanimani Mountains, between Bundi Plain and Upper Valley, shade of small forest patch by stream, flowers mauve with darker spots, 9.IV.1967, *Drummond* 9130 (SRGH).

5. *Brownleea parviflora* Harv. ex Lindl. in Hook. Lond. J. Bot. **1**: 16 (1842). Type: Eastern Cape Province, near King William's Town, 1841, *Brownlee s.n.* (K!, holotype).

Disa parviflora (Harv. ex Lindl.) Reichb.f., Otia Bot. Hamb. **2**: 119 (1881).

Disa alpina Hook.f. in J. Linn. Soc. **7**: 220 (1864). Type: Cameroon Mountain, November, *Mann s.n.* (K!, holotype; W!).

Brownleea alpina (Hook.f.) N.E. Br. in Fl. Trop. Afr. **7**: 287 (1898).

Disa preussii Kraenzl. in Bot. Jahrb. **17**: 64 (1863). Type: Cameroun, grassy area of mountains west of Buea, September. *Preuss* 973 (B†, holotype; K!).

Disa apetalata Kraenzl. in Bot. Jahrb. **22**: 21 (1896). Type: Tanzania, Kilimanjaro, Useri, *Volkens* 1969 (B†, holotype).

Brownleea apetalata (Kraenzl.) N.E. Br. in Fl. Trop. Afr. **7**: 287 (1898).

Brownleea gracilis Schltr. in Bot. Jahrb. **53**: 545 (1915). Type: Tanzania, montane meadows on Rungwe, December 1912. *Stolz* 1178; same locality, April 1913, *Stolz* 1981; meadows at Mpolato, March 1914, *Stolz* 2580 (B†; syntypes, K!, W!, G!, C!, S!, P!, Z!, BM!, PRÉ!, BR!).

Brownleea perrieri Schltr. in Fedde Repert. Beih. **33**: 102 (1924a). Type: Madagascar, Massif d'Andringitra, April 1921. *De la Bathie* 13752; Rocailles de la Manondona, April 1912, *Perrier de la Bathie* 11881 (P!; syntypes).

Brownleea transvaalensis Schltr. in Ann. Transv. Mus. **10**: 250 (1924). Types: Transvaal, Houtboschberg, *Schlechter* 4711 (B†, syntype; Z! K!), Transvaal, Bar-

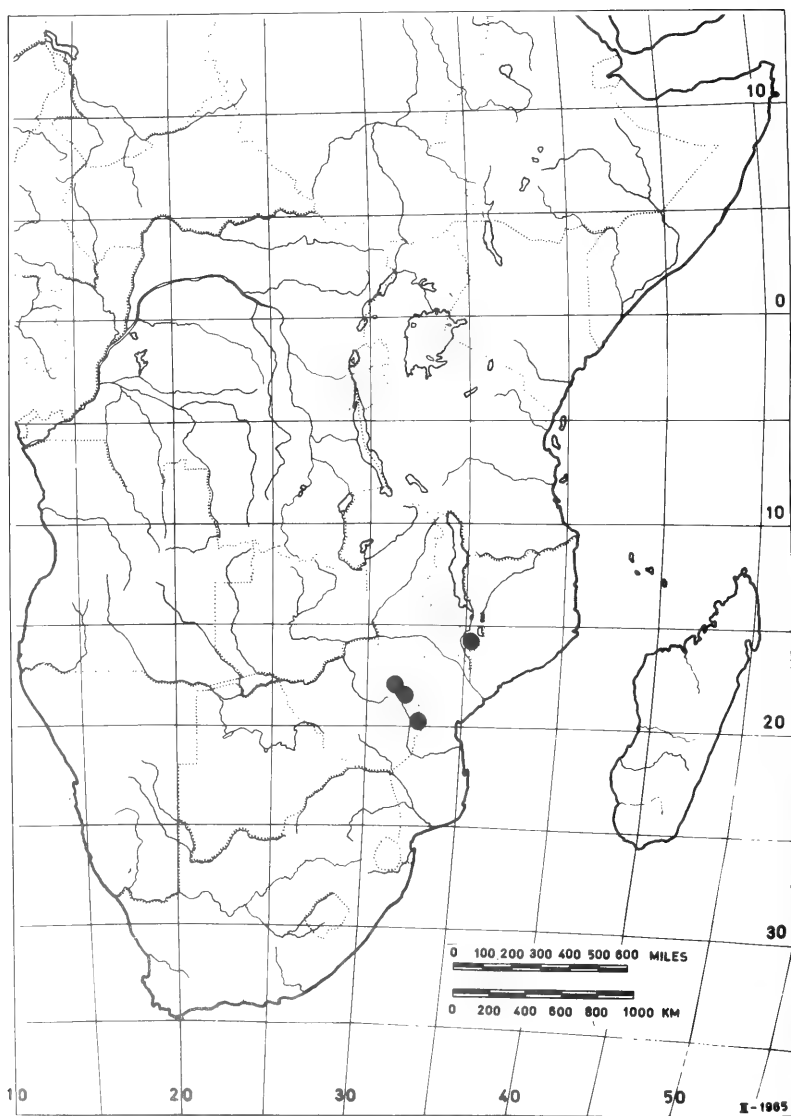


FIG. 8.
Distribution of *B. maculata*.

berton, *Culver* 49 (B†, syntype), Barberton, *Galpin* 1229 (B†, syntype; PRE!, Z!).

Icon: *Icones Orch. Austro-Afr.* 1: t.43 (1896).

Flowers small (lateral sepal 2–5 mm long); spur sharply decurved, 3–5 mm long; inflorescence a dense spike; leaves narrowly lanceolate to rarely lanceolate.

Tubers 15–30 mm long and 10–25 mm in diameter, hirsute. *Plant* 200–600 mm tall, erect, occasionally with fibrous leaf remains at the base; basal sheaths two, the outer up to 30 mm long, often lost; the inner 40–120 mm long, muricate or scabrid. *Leaves* (2–)3(–5), the leaf base sheathing, the blade narrowly lanceolate to rarely lanceolate, semi-erect, very acute to acuminate, the longest leaf at the base, 80–200 mm long and 8–16(–25) mm wide, the leaves grading apically into the floral bracts, the midrib and often the side veins prominent below. *Inflorescence* slender cylindrical, densely 20–60-flowered, 40–120 mm long; ovary (5–)7–8(–10) mm long; bracts narrowly lanceolate to lanceolate, acuminate, erect, taller to very much taller than the flowers and more or less prominent; flowers c. 4 mm in diameter, often facing down, white with a slight green or brown tint. *Dorsal sepal* erect, falcate in side view, ovate, acuminate, galea (2–)3–5 mm tall, 1,5–2 mm wide and 0,8–1 mm deep; spur from a horizontal base, cylindrical, soon sharply decurved, frequently clavate, 3–5 mm long, 0,5–1 mm in diameter at the base and 0,5–2 mm in diameter at the apex. *Lateral sepals* oblique, oblong, acute, spreading forwards, flat with the apical margins somewhat incurved, the bases of the lateral sepals frequently fused, (2–)3–5 mm long and (1–)1,5–2,5 mm wide. *Petals* oblong to almost square in outline, obliquely acute, the nerve falcate, (1,5–)2,5–3,5 mm tall and 1,5–2,5 mm wide. *Lip* minute, 0,5–1 mm long. *Rostellum* c. 1 mm tall, lateral lobes well developed, concave, bearing the viscidia, staminodes half as tall to as tall as the lateral lobes; anther horizontal or somewhat erect, c. 0,8 mm long; stigma shortly stipitate, almost horizontal. (Fig. 9).

The nomenclatural confusion created by the description of a separate species for each geographic area in which this widespread species occurs, and even the description of several species in the same area by taxonomists such as Kraenzlin and Schlechter in his old age, has been mostly clarified by Summerhayes (1966). Summerhayes did not take the Madagascan species into account.

B. parviflora was described by Lindley from a specimen collected at the southern extreme of the distribution range of this species. It is therefore scarcely surprising that Hooker described the collection from the Cameroons as a new species. However, Kraenzlin's description of *D. preussii* is surprising. It appears as if he completely misunderstood the floral structure of the species, as he compared his new species to *Disa polygonoides* and *D. welwitschii*—both species from *Disa* Sect. *Micranthae*.

The type of *D. apetala* is lost. Kraenzlin noted that the specimen was without

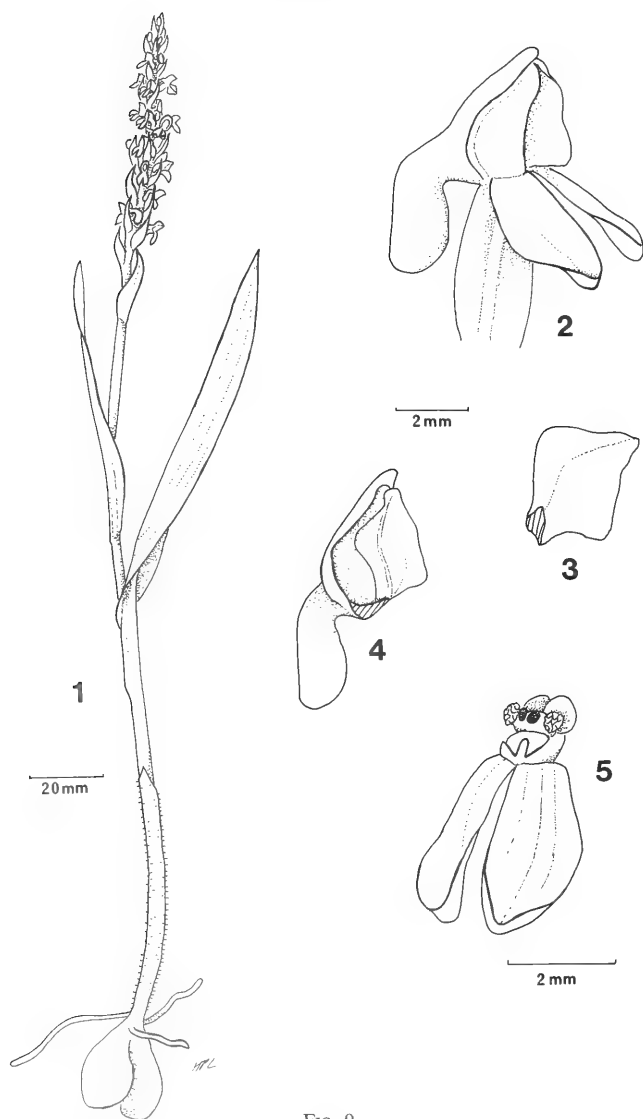


FIG. 9.

B. parviflora. 1. Whole plant (Linder 2074). 2–5. Floral detail (Wild 4472); 2. Whole flower; 3. Petal in two dimensions; 4. Petal and dorsal sepal; 5. Lateral sepals, lip and column.

petals, and suggested that the petals might be fused to the lateral sepals. From the description of the sepals and the spur it is clear that this name is applicable to *B. parviflora*.

Bolus (1889), Kraenzlin (1900), Schlechter (1901) and Rolfe (1913) kept *B. parviflora* distinct from the tropical names, although Schlechter noted that they are very closely allied, and separated by the more slender habit and cylindrical spurs of the tropical species.

Brown (1898) united *B. alpina* and *D. preussii*, but kept *B. apetalata* distinct. Schlechter (1901) united all three species. Kraenzlin (1900) retained *Disa apetalata*; it appears as though he did not understand the concept of *Brownleea* at all. The last tropical species to be described was *B. gracilis*, which Schlechter compared to *B. apetalata*. Schlechter also described *B. transvaalensis* from South Africa. The type is indistinguishable from *B. parviflora*. In 1924 Schlechter described *B. perrieri* from Madagascar. Although he mentioned the affinity of his new species with *B. parviflora*, he did not indicate whether he considered the affinity to be close. It appears as if Schlechter developed a rather narrow species concept in his later years.

VARIATION

As could be expected of such a widespread species, *B. parviflora* shows extensive variation. In the past, insufficient material obscured the continuity in the variation and this led to the description of numerous species.

The spur varies from strongly clavate to slender. Only the slender form has been recorded from the Cameroons (although not much material is available from this area). In East and South-central Africa subclavate spurs do occur. Strongly clavate spurs (spur 1.5–2 mm in diameter at the apex) are only recorded from South Africa (i.e. McLoughlin 63). Material from the same plant can frequently show a remarkable range of variation, and the complete range from clavate to slender spurs can be found in a single population in South Africa.

In general the spur is sharply decurved, but occasionally it is only gently decurved. This latter form is relatively more frequent in tropical Africa than in South Africa.

The lateral sepals are in some cases more or less adnate to one another near the base. This character state is the most frequent in tropical Africa, and very rare in South Africa (i.e. Flanagan 2254). The floral bracts are always longer than the flower, but usually only just overtopping the flowers. In the Rungwe-Isoka area of Tanzania, the bracts are very prominent, up to twice as long or even longer than the ovary, and erect (i.e. the type of *B. gracilis* Schltr.). Intermediate forms are widespread, and occasional forms with long bracts occur in South Africa.

The general robustness of the plant is variable. The leaf width can vary from 10 mm to 30 mm, and the inflorescences from slender (i.e. material from the

Cameroun Mountains, less than 10 mm in diameter) to very densely flowered, cylindrical and robust (i.e. in South Africa, more than 20 mm in diameter).

None of the characters show clear geographic segregation, but whether even detailed population studies would find a basis for the separation of geographical subspecies is doubtful.

ECOLOGY AND PHYTOGEOGRAPHY

This widespread species occurs throughout the Afro-montane Region as defined by White (1978) from southern Tanzania southwards, with outliers on the Cameroun Mountains and on Mt. Nyira in the Northern Frontier Province of Kenya. It also occurs in the montane zone in Madagascar.

Over the whole range the species has been recorded from secondary mountain grassland, sometimes from grassland among the rocks (*Hilliard & Burt* 1970) or from damp grassland. From the little data available, it appears as if the habitat in Madagascar might be different. *Perrier de la Bâthie* (11882) noted that the species grew in rocky areas among *Philippia* bushes, in the altitude range from 1 400 to 2 200 m. This zone is comparable with the Afro-montane zone in Africa (*vide* Koechlin, 1972).

The climate over the range of *B. parviflora* is generally temperate, with rare or no snowfalls. The rain falls mostly in summer, and rainfall ranges from about 1 000 mm p.a. in the southern part of the range, to probably over 2 000 mm p.a. in the Cameroun Mountains (Jackson, 1961). In southern Tanzania the rainfall is c. 1 700 mm p.a., the bulk of which falls between December and April (Kerfoot, 1964). On the Nyika plateau the rainfall varies from c. 1 000 mm to 2 300 mm p.a., depending on the locality (Chapman & White, 1970). In Malawi and Tanzania mists frequently occur in the summer months. In South Africa mists are rare (Killick, 1963).

The flowering time of this species is generally in March, with occasional flowering specimens collected in February or April. Towards the north the flowering time tends to be later.

REPRESENTATIVE COLLECTIONS

Madagascar, Rocailles de la Manondana, fleurs roses, IV.1912, *Perrier de la Bâthie* 11882 (P); Tanzania, Mbeya mountain, bog by stream, upland grassland, 2 340 m, dorsal sepal very pale greenish mauve, petals and labellum almost white, 13.V.1956, *Milne-Redhead & Taylor* 10326 (K); Malawi, Nyika, Kasaramba road, 2 400 m, grassland, flowers purple, 28.III.1970, *Pawek* 3392 (K); Zambia, Nyika Plateau, grassland, III.1967, *Williamson & Odgers* 297 (SRGH, K); Zimbabwe, Umtali, Himalaya Range, Engwa Peak, 2 100 m, sparse grassland, flowers white, 3.III.1954, *Wild* 4482 (SRGH, K); Transvaal, Carolina to Lydenburg, sandy soil, grassland, 11.III.1939, *Dyer* 3851 (PRE, K); Cape,

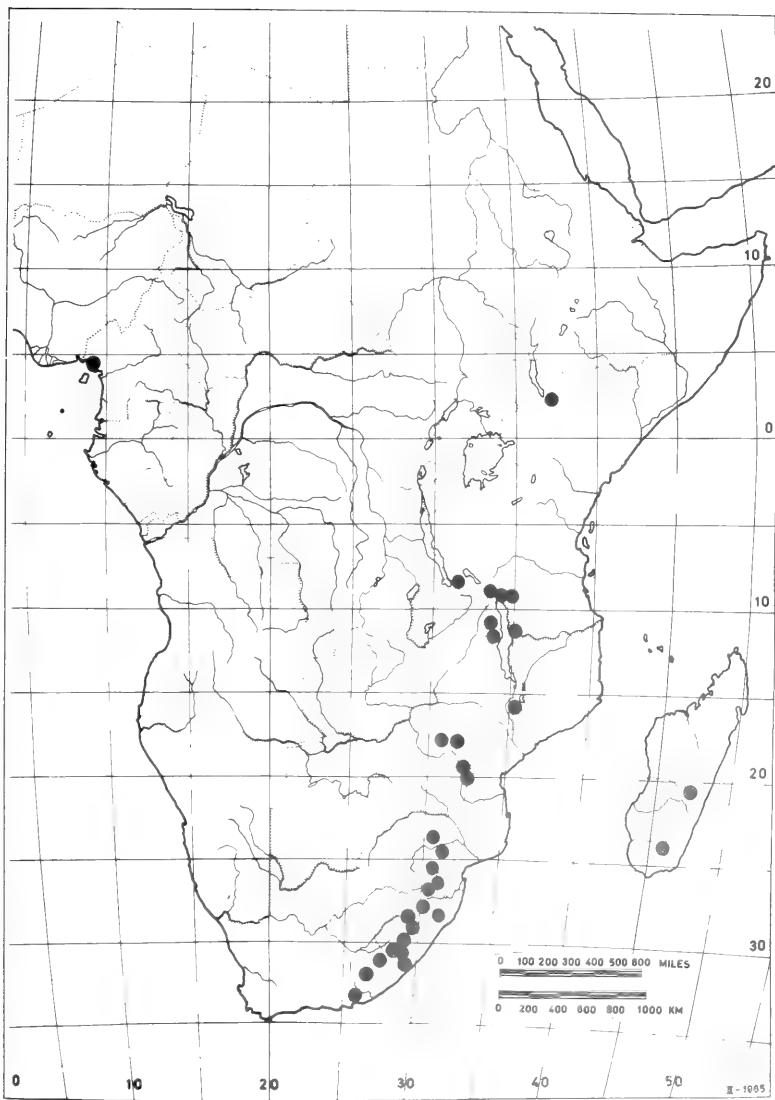


FIG. 10.
Distribution of *B. parviflora*.

Somerset East, upper slopes of Boschberg, III.1869, *MacOwan 1530* (BOL, BM, PRE, K, SAM, Z, ZT, W).

6. *Brownleea galpinii* Bolus, *Icones Orch. Austro-Afr.* 1: t.42 (1893). Type: Natal, banks of streams near Kokstad, alt. 1 540 m, March, *Tyson 1084* (BOL!, syntype; K!, SAM!, GRA!), Transvaal, between Barberton and Swaziland, 1 400 m, March, *Galpin 1255* (BOL!, syntype; K!, Z!, PRE!, SAM!). *Galpin 1255* (BOL) is here selected as the lectotype.

Brownleea flavescens Schltr. in *Ann. Transv. Mus.* 10: 249 (1924). Type: Eastern Transvaal, in marshes in Houtboschberg, February 1894, *Schlechter 4391* (B†, holotype; BOL!, GRA!, K!, PRE!, BM!, G!, Z!, W!, BR!).

Icon: Bolus, *Icones Orch. Austro-Afr.* 1: t.42 (1893).

Flowers aggregated in dense capitate inflorescences; spurs almost straight, 3–6 mm long; petals oblong-pandurate with expanded crenate upper margins.

Tubers usually more or less globular, 10–20 mm in diameter, villous. *Plant* occasionally subflexuose, 150–300–500 mm tall; basal sheaths often two, the inner 50–100(–140) mm long, acute, ribbed, pale brown, often more or less mottled with small mucronate patches. *Leaves* 2(–4), usually scattered on the upper half of the stem, erect to semi-erect, linear, the leaf base sheathing, the blade very acute, subconduplicate, the lowest leaf 60–200 mm long and 5–15 mm wide with prominent ribs, the upper leaf much smaller than the lower leaf. *Inflorescence* capitate, often secund, 15–45 mm long and 10–30 mm in diameter, 5–25-flowered; bracts lanceolate, acuminate, somewhat longer than the ovary; ovary c. 10 mm long; flowers facing out horizontally, c. 5 mm in diameter, white to cream, the petals frequently with small purplish spots on the “fan”. *Dorsal sepal* galeate, erect, narrowly ovate to lanceolate, falcate in side view, acuminate, galea 5–10 mm tall and c. 2 mm deep; spur slender cylindrical obtuse, 3.5–4.8–6 mm long, parallel to the ovary, straight. *Lateral sepals* suboblique, narrowly elliptical, acute, spreading forwards, flat, the apex often down-curved, 6–7.4–10 mm long and 2–4 mm wide. *Petals* almost as tall as the dorsal sepal, narrowly oblong-pandurate in outline, the basal anticus lobe flanking the stigma and the apical lobe spreading fan-like, variable in size and crenulation and up to 4 mm wide. *Lip* minute, erect, 0.8–2.5 mm long, linear. *Rostellum* erect, c. 3 mm tall, the lateral lobes narrowly oblong and shallowly grooved, central lobe subobsolete, staminodes c. 1 mm in diameter; anther horizontal at the base, then upcurved so that the apex frequently touches the rostellum; stigma vertical, sessile at the base of the rostellum.

TAXONOMIC NOTES

When Bolus described *Brownleea galpinii*, he also described a var. *major*, which he differentiated from the typical variety by: “floribus plus quam quarta parte majoribus; petalis latioribus apice rotundatis, magis lobatis concavisque;

labello duplo longiore". This was accepted by subsequent authors, until Schlechter raised the variety to specific level in 1924.

Unfortunately only some 30 collections of *B. galpinii* were available for study, and field studies have only been conducted on one of the subspecies (*B. galpinii* ssp. *major*). Analysis of the available material revealed that the two putative taxa show some size segregation (length of the lateral sepals, see Fig. 11) in the flowers, and that the lip is twice as long in the ssp. *major*. Remark-

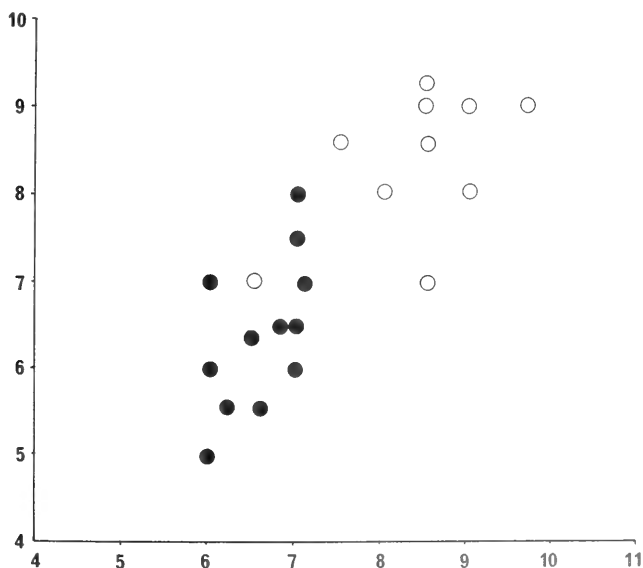


FIG. 11.

Variation in lateral sepal length and lip length in *B. galpinii*. Open circles represent *B. galpinii* ssp. *major*, and solid circles *B. galpinii* ssp. *galpinii*.

ably, spur length remains almost constant throughout the species. Petal shape variation is correlated with lip and flower size variation, but is difficult to quantify. In the ssp. *major*, the apical lobe of the petal is more expanded and the margin is more crenulate than in the typical subspecies.

The two collections from Mt. Marwaga in Natal (2929-DC) (O'Connor 344 and Rennie 348) indicate that populations on this mountain might be intermediate between the two subspecies.

The two subspecies are allopatric, with ssp. *galpinii* extending from East Griqualand to Inyanga in Zimbabwe, and ssp. *major* restricted to the Drakensberg in Natal and Lesotho. Along the contact zone, ssp. *major* appears to occur at higher altitudes than ssp. *galpinii*.

These two taxa therefore appear to be eco-geographic subspecies, with some morphological differentiation.

6a. ***Brownleea galpinii* Bolus ssp. *galpinii***

Flowers smaller, lateral sepals 6–7 mm long and dorsal sepal 5–8 mm long; petals with the upper margin not or slightly crenulate; lip erect, 0.8–1.3 mm long, not reaching the top of the stigma.

The one syntype of *B. galpinii* (Tyson 1084) is from the southern extreme of the distribution range of this subspecies.

B. flavescens was described from Schlechter 4391, which was collected from near the centre of the distribution range of *B. galpinii* ssp. *galpinii*. Schlechter (1924b) differentiated it from *B. galpinii* and *B. leucantha* (= *B. galpinii* ssp. *major*) on the basis of its having three leaves (which not all individuals in the collection have), "oblogoid" inflorescences (the meaning of this term is not clear), smaller flowers, narrower petals and a shorter spur. The latter characters fit *B. galpinii* ssp. *galpinii*. There is no doubt that the species has to be included in *B. galpinii* ssp. *galpinii*.

ECOLOGY AND PHYTOGEOGRAPHY

This subspecies occurs in the escarpment mountains from Zimbabwe to the Van Reenen gap between the Natal and Transvaal Drakensberg. From there it extends into the Natal uplands to East Griqualand. In this latter area it appears to be quite rare.

The distribution area could be described as montane, with a more or less temperate climate and with snow only occurring rarely. The rainfall occurs mainly in summer, and is about 1 000 mm p.a. The altitude at which the subspecies occurs increases from 1 540 m in the south at Kokstad to 1 300–2 200 m in the Eastern Transvaal to up to 2 500 m in Zimbabwe.

In general this taxon has been recorded from damp grassland, stream banks or seepages, although there are some records from rocky areas (Jacobson 3806, from Inyanga in Zimbabwe and Davidson 3120 from rock crevices on Wolkberg in the Eastern Transvaal).

Flowering occurs in March and April, with a few records of flowering as early as February.

REPRESENTATIVE COLLECTIONS

Transvaal, Bosch's near Barberton, 1 350 m, flowers white, III.1891, *Galpin* 1255 (SAM, BOL, PRE); Natal, Ngome, above forest, damp grassland, 1 200 m

flowers pure white, 2.IV.1977, *Hilliard & Burt* 9938 (NU); Zimbabwe, summit of Mt. Inyangani, 2 400 m, flowers white, 14.II.1931, *Norlin* & *Weimarck* 5001 (K, SRGH, S, BR).

6b. *Brownleea galpinii* Bolus ssp. *major* (Bolus) Linder, stat. nov.

Basionym: *Brownleea galpinii* Bolus var. *major* Bolus, *Icones Orch. Austro-Afr.* 1: t.42 (1893). Type: Natal, south side of Mount Currie, near Kokstad, March, *Tyson* 1074 (BOL!, holotype).

Brownleea fanniniae Rolfe in *Kew Bull.* 1920: 131 (1920). Type: Natal, Dargle Farm, *Mrs Fannin* 98 (TCD!, holotype).

Brownleea leucantha Schltr. in *Ann. Transv. Mus.* 10: 249 (1924b). Type: As for *B. galpinii* Bolus var. *major* Bolus.

Icon: Bolus, *Icones Orch. Austro-Afr.* 1: t.42 (1893).

Flowers large, lateral sepals (6,5–)8–10 mm long. and dorsal sepal 7,5–9 mm long; petals with the apical lobe crenulate and fan-like; lip 2–2,6 mm long, reaching over the stigma to between the rostellum lobes. (Fig. 12).

When Bolus described *B. galpinii* in 1893, he also described the var. *major*, and commented: "The variety *major* looks at first sight different, but there are too many points of identity to justify specific distinction." This view is still valid.

Rolfe (1920) noted about *B. fanniniae* that "*B. galpinii* . . . must be very nearly allied, but I have not seen a specimen". Reference to *Flora Capensis* shows that this must refer to *B. galpinii* var. *major*, as he had cited as having seen material of var. *galpinii*. The type sheet holds two very well-preserved specimens of this rather beautiful species.

In 1924 Schlechter raised *B. galpinii* var. *major* to specific status, and named it *B. leucantha*. For reasons given above, this view is not held here.

ECOLOGY AND PHYTOGEOGRAPHY

This subspecies is restricted to the Sub-Alpine belt (*vide* Killick, 1963) of the Natal Drakensberg, from Matatiele in the south to Mont-aux-Sources in the north.

The altitudinal range of the subspecies is from 1 800 m to about 2 500 m. In this zone this taxon occurs in grassland or in open *Protea* savanna, in basaltic or sandstone derived soil (Killick, 1963; West, 1951). The climate is cold temperate, with snowfalls in winter. The rainfall in the Cathedral Peak area ranges from 1 400 mm at the lower altitudes to almost 2 000 mm at the upper altitudes (Killick, 1963). The rain falls mainly in the summer months, when fog also frequently occurs.

In damp areas this species tends to form fairly sparse to almost dense populations. Field studies in the Mont-aux-Sources area showed that the subspecies extended from 1 800 m to 2 500 m, and tended to form small populations in damp seepage areas. At higher altitudes where the grassland was seasonally wet-

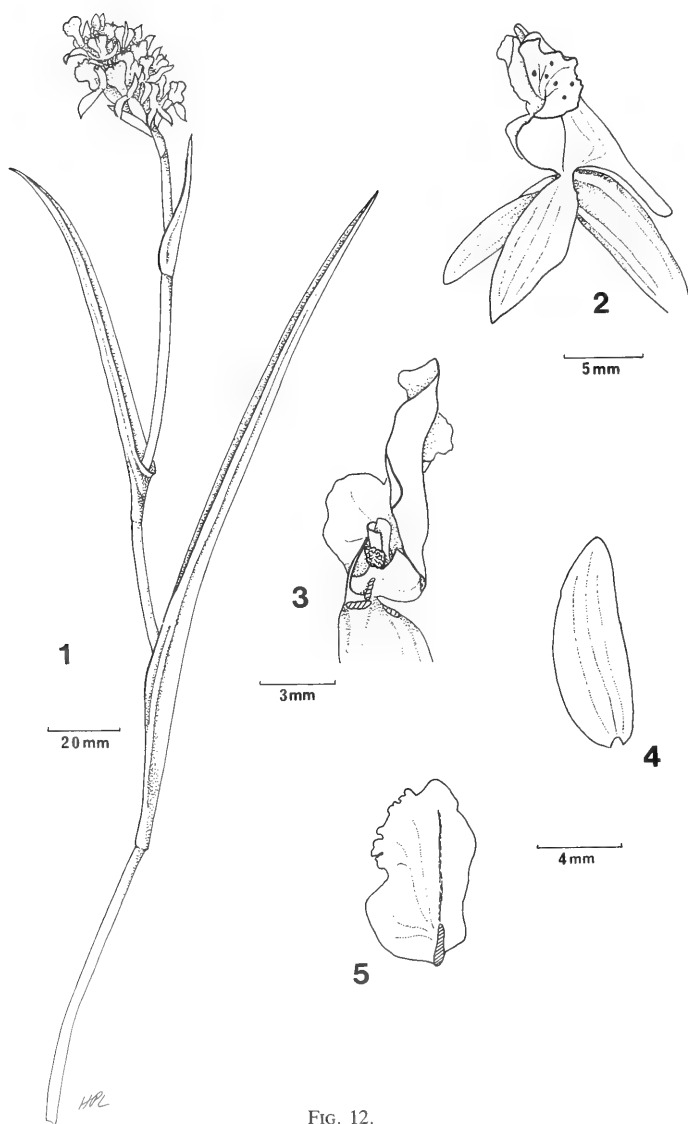


FIG. 12.

B. galpinii ssp. *major*. 1. Whole plant (Linder 2073). 2–5. Floral detail (Fannin 98); 2. Whole flower; 3. Petal, lip and column; 4. Lateral sepal (flattened); 5. Petal (flattened).

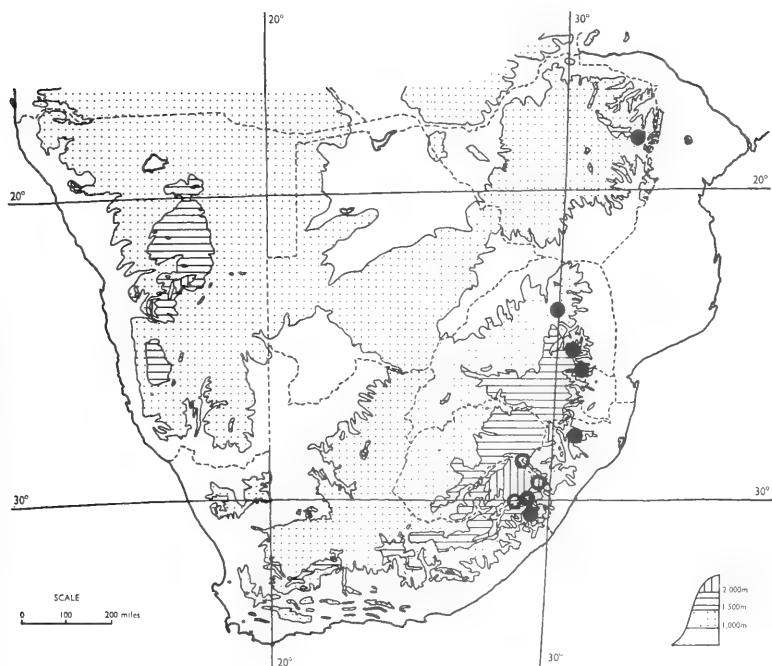


FIG. 13.

Distribution of *B. galpinii*. Open circles represent *B. galpinii* ssp. *major* and solid circles represent ssp. *galpinii*.

ter, populations tended to be extensive. The same tendencies were observed in the Sehlabathebe National Park, Lesotho.

Flowering occurs from the end of January to March.

REPRESENTATIVE COLLECTIONS

Lesotho, Sehlabathebe, near summit of Bushmansnek Pass, c. 2 500 m, flowers pure white, petals with a couple of purplish spots on the "fan"; no detectable scent, locally common in damp grassland. 27.II.1979. *Linder 2093* (BOL): Natal, Mont-aux-Sources, 2 400 m, damp seepage areas, labellum and sepals creamy white, 4.III.1977, *Rourke 1534* (BOL).

SPECIES EXCLUDED

Brownleea pentherana Kraenzl. in Ann. Nat. Hofmus. Wien **20**: 6 (1905).
Type: Montagu Pass. 2.XI.1894, *Penther 189* (W!, holotype).

This is a synonym of *Monadenia ophrydea* Lindl. in Gen. Sp. Orch. 358 (1838).

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APPENDIX 1. LIST OF SPECIMENS STUDIED

The specimens are listed alphabetically according to the name of the collector. The figures in brackets refer to the number of the taxon in the text. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren and Keuken (1974). Hybrid collections are indicated by combinations such as (2–5).

Acocals 22072 (5) PRE—Adamson 434 (5) BM, K—Alleizette 621 (2) P—Allen 526 (5) K; 528 (4) K—Atherstone 30 (2) K.

Ball 47 (4) SRGH; 283 (5) SRGH; 1028 (5) SRGH; 1029 (5) SRGH; in SRGH 50961 (4) K—Barber (2) Z; (5) K—Baron 1751 (2) K; (2) K—Baur 625 (3) BOL, K; 638 (2) G—Bayer & McClean 285 (1) PRE—Beasley 52 (6a) K, SRGH; 73 (5) SRGH; 74 (6a) K, SRGH—Benson 1263 (5) K—Bernardi 8915 (2) G, K—Beverley 493 (1) NU—Beverley & Hoener 623 (6b) NU; 679 (5) NU—Boardman 42 (5) PRE; 260 (5) PRE; 273 (5) BOL—Bokelmann (1) BOL—Bolus 10295 (5) BOL; 10296 (5) BOL—Bos er 11085 (2) P; 10312 (2) P; 19507 (5) P—Bredenkamp 783 (5) PRE—Brooke 51 (5) BM—Brownlee (2) K; (5) K; in Tyson 2918 (2) SAM—Buchanan (5) K—Button 58 (5) NU.

Chase 217 (4) SRGH; 6013 (5) K, SRGH; 4069 (5) SRGH; 4494 (4) SRGH—Codd 9314 (2) PRE—Compton 21636 (2) NBG, PRE; 25811 (2) NBG, PRE; 26730 (2) NBG, PRE; 28560 (2) NBG—Cribb & Grey-Wilson 10823 (5) K—Culver (2) K—Cuthbert 32 (5) K—Davidson 3120 (6a) BOL—Decary 13321 (2) P—De Souza 533 (2) PRE—Devenish 1314 (5) G, K, PRE—Dieterlen 765 (5) K, P, PRE, SAM, Z; 906 (1) PRE—Doe 17 (3) BOL; 24 (2) BOL; in BOL 23637 (1) BOL; (3) BOL—Doidge 4797 (5) K—Drège (1) G;

(3) SAM; (5) G—Drewe 11 (5) K—Drummond 9130 (4) SRGH; 9143 (5) SRGH; 9161 (5) SRGH—Dusein 438 (5) S—Dyer 3951 (5) K, PRE.

Ecklon & Zeyher (5) P, S—Edwards 4302 (2) K, PRE—Esterhuysen 16856 (3) BOL; 27149 (3) PRE; (3) NBG.

Ferrar 3984 (5) PRE, SRGH—Flanagan 529 (2) PRE, SAM, Z; 2254 (5) K, PRE; 2254a (3) K; 2256 (3) P, PRE, SAM, W; 2549 (5) P; 2876 (5) PRE—Fourcade 554 (3) BOL—Fox 3 (2) K—Francois (2) P—Fuller 107 (5) K; 133 (5) K.

Galpin 1229 (5) PRE, Z; 1255 (6a) BOL, PRE, SAM; 1257 (2) PRE; 1506 (5) PRE; 2056 (3) PRE; 6839 (1) PRE; 6840 (3) BOL, K, PRE; 8182 (5) K; (6a) BOL—Germishuizen 45 (2) PRE—Gilliland 1895 (6a) BM, K; 1899 (5) K—Glass 521 (5) Z; 893 (1) SAM; in MacOwan & Bolus 1377 (3) BM, BOL, K, SAM, UPS, W—Gower (5) PRE—Grewcock in PRE 20151 (2) PRE—Grice (5) NU; (6b) NU—Grosvenor 834 (5) SRGH—Grosvenor & Renz 1195 (5) SRGH; 1331 (5) SRGH—Guillarmod 1143 (1) PRE.

Hamilton (2) PRE—Harrison in BOL 25769 (2) BOL—Harvey 22 (2) K; 107 (2) K; (2) BOL—Hilliard 2749 (2) NU; 8116 (5) NU—Hilliard & Burtt 6508 (3) K, NU, PRE; 6630 (1) K, NU; 9938 (6a) NU; 9970 (5) BOL, NU—Holland in BOL 23638 (2) BOL—Humbert 15073 (5) P; 15101 (5) P; 20883 (2) P—Hutton (2) K; (2) K; (3) K, Z; (5) K, S.

Jackson 2182 (5) K—Jacobsen 2655 (2) PRE; 3799 (5) K, PRE, SRGH; 3806 (6a) K, PRE, SRGH—Jacobsz 577 (5) PRE; 2114 (5) NBG; 2586 (5) PRE; (5) BOL—Jacot Guillarmod 2503 (1) PRE; 4018 (1) PRE—Jacottet 67 (5) Z—Jeppe in PRE 33351 (3) PRE—Johnston 86 (5) BM, K; (2) NBG—Jones 68 (5) SRGH—Junod 1209 (5) G; (5) G.

Kerfoot 2100 (5) K—Killick 1905 (5) PRE; 2319 (1) BM, K, PRE; 3920 (2) PRE—Krook 90 (5) W.

Laughton 163 (3) BOL—Leipoldt (3) BOL—Levey 2822 (2) PRE—Linder 912 (1) BOL; 949 (1) BOL; 1008 (1) BOL; 1017 (1) BOL; 1042 (1) BOL; 1051 (1) BOL; 1055 (1) BOL; 1067 (1) BOL; 1072 (1) BOL; 1079 (1) BOL; 1767 (3) BOL; 2051 (2) BOL; 2072 (6b) BOL; 2073 (6b) BOL; 2074 (5) BOL; 2075 (1) BOL; 2093 (6b) BOL; 2094 (3) BOL; 2110 (3) BOL; 2111 (1) BOL.

MacInnes 215 (5) K—MacOwan 232 (2) BOL, K, S, SAM, W, Z; 526 (3) BOL, BM, G, K, SAM, W, Z, ZT; 1530 (5) BM, BOL, K, PRE, SAM, W, Z, ZT—MacOwan & Bolus 1377 (3) BM, BOL, G, K, P, SAM, UPS, W, ZT—Mann 2120 (5) K—Marloth 6027 (3) PRE—McChan 253 (5) PRE—McCloughlan 10 (5) BOL; 23 (5) BOL; 63 in PRE 12755 (5) PRE; 68 in PRE 12757 (2) BOL, PRE; 194 (1) BOL; 195 (6b) BOL; 205 (3) BOL; 211 (5) BOL; 223 (5) BOL; 531 (5) BOL, PRE; in BOL 16403 (1) BOL; (3) BOL; (5) PRE; (5) BOL; (5) PRE—Meikle (4) SRGH—Milford 701 (1) K—Milne-Redhead & Taylor 10326 (5) K; 10390 (5) K—Meuller 2662 (4) SRGH.

Newdigate 252 (3) BOL—Newton & Whitmore 403 (4) BM—Nicholson 1528 (2) PRE; 1529 (2) PRE—Norlindh & Weimarck 5001 (6a) BR, K, S, SRGH.

O'Connor 344 (5) NU; 344 (6b) NU; 369 (2) NU.

Pappe (2) K, SAM; in SAM 27428 (5) SAM—Pawek 2197 (5) K; 3392 (5) K; 4646 (5) K; 9284 (5) K; Pegler 820 (2) PRE, SAM; 2056 (5) PRE—Pegler & Kolbe (3) BOL—Peltier 2187 (2) P; 5363 (2) P; 5405 (2) P—Perrier de la Bâthie 11882 (5) P; 13505 (2) P; 13701 (2) P; 14713 (2) P—Physick 45 (6b) NU—Plowes 2852 (4) SRGH—Potter 1799 (5) PRE—Preuss 973 (3) K.

Rand 1201 (5) BM—Ranger 20 (2) PRE—Rehman 2850 (2) Z; (3) Z—Rennie 348 (6a) NU; 820 (6b) NU—Richards 13791 (5) BR, K—Richardson 102 (6a) NU; 104 (5) NU—Robinson 4477 (5) K—Rogers 18813 (2) Z—Rourke 1534 (6b) BOL—Rudatis 1357 (2) BM, G, K, P, PRE, W, Z—Rutgers 13 (5) BOL.

Schelpel 1425 (6b) NU; in NBG 361/56 (2) NBG—Schlechter 2540 (5) PRE; 4391 (6a) BM, BOL, BR, G, GRA, K, W, Z; 4711 (5) K, Z; 6942 (5) Z—Schlieben 907 (5) BR, G, Z—Schofield (5) NU—Schweikerdt in PRE 31851 (5) PRE—Scott-Elliot 483 (3) BM; 913 (2) BM, K—Scully 411 (2) Z—Semsei 1680 (5) K—Sidey 1602 (5) PRE, S—Sim 14 (2) BOL; 21 (3) Z; 23 (3) BOL; 257 (5) PRE; 869 (5) NU; 870 (2) NU; 2979 (5) NBG; (3) NBG—Simon & Kelly 1851 (4) BOL, SRGH—St. Clair Thompson 795 (5) K; 907 (5) K; 914 (5) K—Steward 2054 (5) NU—Stirton 1762 (2) PRE; 1773 (5) PRE; 1816 (2) K.

PRE—Stolz 1178 (5) K; 1981 (5) K; 2580 (5) BM, BR, C, G, K, P, PRE, S, W, Z—Strey 2989 (2) K, PRE; 3707 (2) PRE; 6503 (2) PRE; 7425 (2) PRE—Symons 418 (1) PRE.

Thode 52 (1) K—Thorncroft 1453 (5) K, PRE; (2) K, PRE—Trauseld 242 (6b) PRE, NU; 347 (5) NU, PRE; 992 (5) PRE—Tyson 1074 (6b) BOL; 1080 (5) BOL, K, SAM; 1084 (6a) BOL, GRA, K, SAM; 2066 (5) K, PRE, SAM, Z; 2680 (5) PRE.

Van der Merwe 1293 (5) PRE—Vet. Officer (3) PRE.

Wall 43 (3) S—Waterlot 789 (2) P; (2) P—Weale 931 (5) BM, W—Weiste (4) SRGH—Whellan 1249 (4) SRGH—Whitworth (3) BOL—Widdicombe 17 (2) BOL; 18 (3) BOL; (5) BOL—Wild 2913 (4) K, SRGH; 4472 (5) K, SRGH; 4482 (5) K, SRGH; 4523 (5) K, SRGH; 5477 (6a) K, SRGH; 5713 (5) BOL, K, SRGH; 6230 (4) BOL, K, SRGH—Williams in PRE 10513 (2) PRE—Williamson & Odgers 294 (5) K, SRGH—Williamson, Ball & Simon 900 (5) SRGH—Wood 971 (5) BM; 1982 (2) K; 3177 (3) K; 3179 (2) K; 7501 (2) BM, PRE; 9278 (6b) GRA, PRE; 9335 (2) G—Wright 1455 (5) NU; 2184 (6b) NU—Wylie in Wood 7501 (2) BM, PRE.

THE AQUATIC HYPHOMYCETES OF THE APIES RIVER, SOUTH AFRICA

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ABSTRACT

To increase our knowledge of South African freshwater Hyphomycetes, a study was done on the Hyphomycetes of the Apies river. This has led to the identification of 18 species representing 10 genera, of which 4 are new records for South Africa and 3 new records for the African continent.

UITTREKSEL

DIE AKWATIESE HIFOMISETE VAN DIE APIESRIVIER, SUID-AFRIKA

Ten einde die kennis van Suid-Afrikaanse varswater hifomisete uit te brei, is 'n ondersoek na die hifomisete van die Apiesrivier gedoen. Hierdie studie het gelei tot die identifisering van 18 spesies wat 10 genusse verteenwoordig, waarvan 4 nuwe rekords vir Suid-Afrika en 3 nuwe rekords vir die Afrika kontinent is.

INTRODUCTION

The hyphomycete flora of fast-flowing rivers has been the subject of extensive taxonomic studies since 1942, when Ingold began a series of publications revealing the diversity of aquatic hyphomycete species. Relatively few reports have come from Southern Africa (Ingold, 1958; 1973) and only one study from South Africa is known (Greathead, 1961) in which 18 records were documented for the Eastern Cape Province.

This study was therefore undertaken to expand on the knowledge of the range of species found in South Africa, and to contribute new records for a more complete distribution pattern of the aquatic Hyphomycetes.

MATERIAL AND METHODS

All samples were collected from the Apies river near Pretoria. The stream flows through rich vegetation and the banks are bordered by deciduous trees, predominantly *Celtis africana* Burm. f., *Combretum erythrophyllum* (Burch.) Sond., *Kiggelaria africana* L., *Populus* spp., and *Salix babylonica* L.f. Grasses such as *Hyparrhenia hirta* (L.) Stapf, *Poa annua* L. and *Setaria chevalieri* Stapf ex Stapf and C. E. Hubb. are also present. Aquatic plants are represented by *Ethulia conyzoides* L. only, which grows predominantly in the shallow waters. The river-bed is principally of gravel.

Submerged leaves, both well-decayed and freshly fallen, were collected at

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regular intervals from March through August. The leaves were immediately taken to the laboratory where they were rinsed with sterile distilled water, placed in sterile Petri dishes with sterile distilled water and incubated at 15 °C (Webster, 1975).

After 24–48 hours the leaves were examined microscopically for hyphomycete growth, and the Petri dish bottom was scanned for settled spores. Foam and scum samples were collected in sterile screw cap bottles, and microscope slides were then prepared in the laboratory using lactophenol cotton blue as a mounting medium. Water samples were also collected and filtered using 13 mm diameter Millipore filters with 8 µm pore size (Iqbal and Webster, 1977). The precipitate on the filters were scraped onto microscope slides and mounted in lactophenol cotton blue.

Cultures were made from incubated leaves and foam samples using flame drawn Pasteurpipettes to transfer single spores on to 2 % Difco malt extract agar with 62,5 mg sodium novobiocin (albamycin-T) per 1 000 cm³ distilled water to inhibit bacterial growth.

Spore development was studied by placing agarstrips of hyphomycete culture in a petri dish containing sterile distilled water. The suspension was aerated by forcing compressed air through a pipette containing sterile cotton wool and allowing the air to bubble through the suspension in the Petri dish. All cultures were kept at 15 °C.

RESULTS

The investigation has resulted in the identification of 18 species representing 10 genera (Table 1). These species are illustrated in Figures 1 and 2. *Alatospora constricta* Dyko, *Camphylospora chaetoclada* Ranzoni, *Lemonniera pseudofloscula* Dyko and *Triscelophorus acuminatus* Nawawi are new records for South Africa and, except for *Camphylospora chaetoclada*, new records for the African continent.

The aquatic Hyphomycetes occurring most frequently are *Tetracladium marchalianum* de Wild., *Tetracladium* sp. and *Triscelophorus acuminatus*. *Lemonniera pseudofloscula* and *Scorpiosporium* sp. were observed only once in one foam sample. *Lunulospora curvula* Ingold and *Tricladium* spp. showed a marked variation in seasonal abundance. *Flagellospora penicillioides* Ingold, *Lunulospora curvula*, *Tetracladium marchalianum* and *Tetracladium* sp. were successfully isolated and cultured.

During March, heavy rainfall occurred and the river flooded occasionally. The number of spores found during that period was low. In early winter, especially during June, there was no rain and in many of the river's tributaries the flow-rate was very low. At times the water became stagnant and rich in algae and bacteria.

The flow of the main river, however, remained continuous. When the water

TABLE 1.

Precipitation, water temperature and seasonal distribution of aquatic Hyphomycetes of the Apies river.

(Occurrence is recorded as follows: ***abundant; **common; *rare)

	March	April	May	June	July	August
<i>Alatospora acuminata</i>	**	**	**	***	***	***
<i>Alatospora constricta</i>		*				
<i>Anguillospora longissima</i>	***	***	***	**	**	**
<i>Articulospora tetraccladia</i>			**	***	***	***
<i>Campylospora chaetocladia</i>		*	**	**	***	***
<i>Flagellospora curvula</i> Ingold		**	**	**	*	*
<i>Flagellospora penicillioides</i>	***	***	***	**	**	**
<i>Lemonnieria pseudofloccula</i>			*			
<i>Lunulospora curvula</i>	***	***	***	**	**	**
<i>Scorpiosporium</i> sp.		*				
<i>Tetracladium marchalianum</i>	***	***	***	***	***	***
<i>Tetracladium setigerum</i>	*	*	*	*	*	*
<i>Tetracladium</i> cf. <i>setigerum</i>	***	***	***	***	***	***
<i>Tricladium gracile</i>				**	**	**
<i>Tricladium splendens</i>			**	**	**	**
<i>Tricladium</i> spp.				***	***	***
<i>Triscelophorus acuminatus</i>		**	***	***	***	***
<i>Triscelophorus monosporus</i>		**	**	**	**	**
Species total	7	13	14	15	15	15
Water temperature (°C)	15,9	10,3	8,6	6,3	5,88	5,44
Precipitation (mm)	59,7	18,1	12,1	0	12,2	16,7

*** abundant: large numbers of the same spore-species found in each sample

** common: the same species found in each sample, but not in large numbers

*rare: single spores found only occasionally in samples

level was high, species such as *Anguillospora longissima* (Sacc & Syd) Ingold, *Flagellospora penicillioides*, *Lunulospora curvula*, *Tetracladium marchalianum* and *Tetracladium* cf. *setigerum* occurred in great abundance. *Articulospora tetraccladia* Ingold, *Alatospora acuminata* Ingold, *Tricladium* spp. and *Triscelophorus acuminatus* were found in large numbers when the water temperature was lowest and the water flow was at a minimum. *Campylospora anachaetocladia* occurred from June to August, but *Lunulospora curvula* and *Flagellospora* spp. were found only occasionally during this period.

DISCUSSION

During autumn and winter (April to August) the abundance of the fungi and the diversity of its species composition increased. This is in agreement with Conway's findings (Conway, 1970). The Apies river is well shaded at the localities that were sampled and this may well contribute to the low water temperature which is certainly a factor in the abundance of the aquatic Hyphomycetes found.

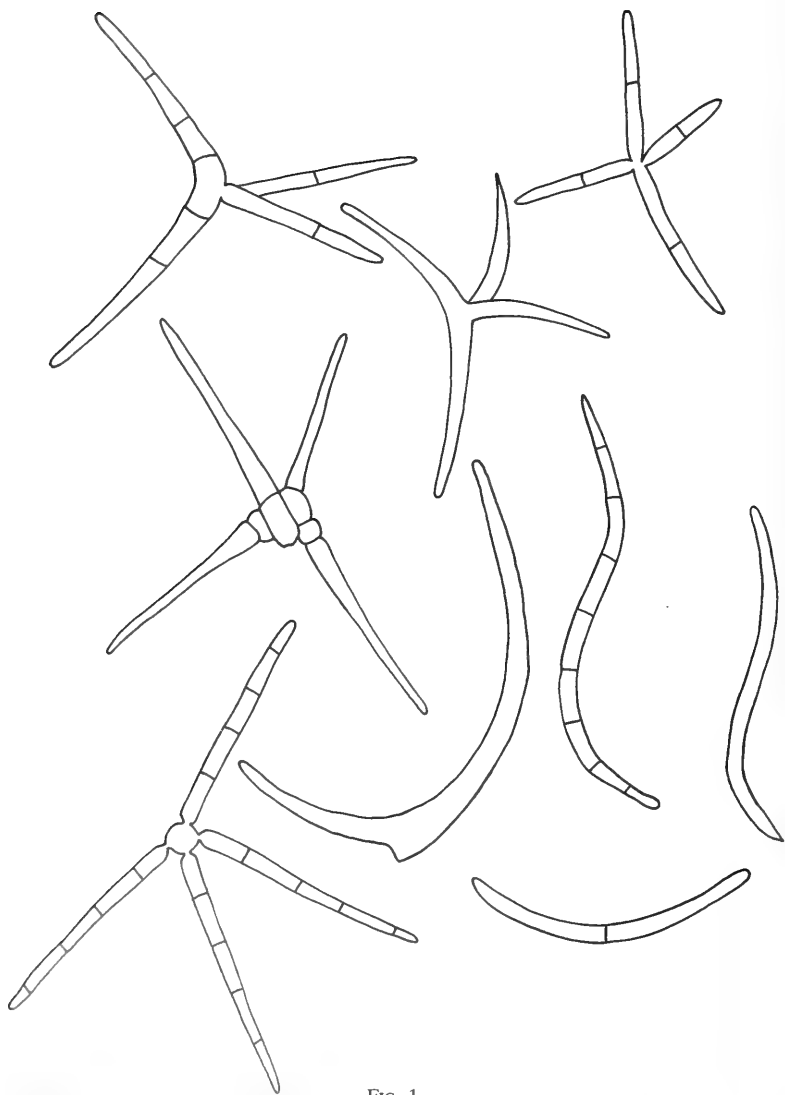


FIG. 1.

Conidiospores of aquatic Hyphomycetes of the Apies river collected from precipitates from filters. 1. *Alatospora acuminata*; 2. *A. constricta*; 3. *Anguillospora longissima*; 4. *Articulospora tetracladia*; 5. *Campylospora chaetocladia*; 6. *Flagellospora curvula*; 7. *F. penicillioides*; 8. *Lemonnieria pseudofloscula*; 9. *Lunulospora curvula*.

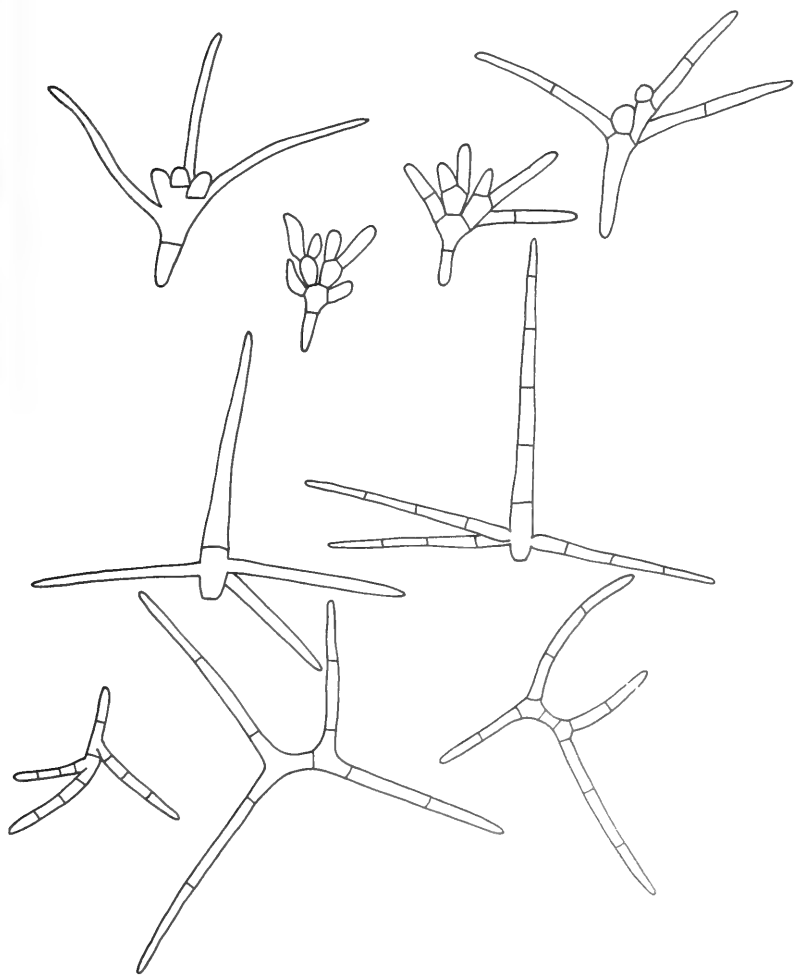


FIG. 2.

Condiospores of aquatic Hyphomycetes of the Apies river collected from precipitates from filters. 1. *Tetracladium marchalianum*; 2. *T. setigerum*; 3. *Tetracladium* cf. *setigerum*; 4. *Tricladium gracile*; 5. *Tricladium splendens*; 6. *Tricladium* sp.; 7. *Triscelophorus acuminatus*; 8. *Triscelophorus monosporus*.

Spores similar in morphology to *Tetracladium setigerum* were found in abundance throughout the period of study (Fig. 2). Cultural studies are still in progress to determine whether it is not in fact a new species of *Tetracladium*. Spores of the typical *T. setigerum* were also found, but only very rarely (Table 1).

Most of the fungi found in the Apies river could be placed into the groupings suggested by Nilsson (1964):

TABLE 2.

The geographical distribution of aquatic Hyphomycetes of the Apies river according to the grouping suggested by Nilsson.

Group A

Worldwide distribution

A.1 Mostly tropical

Campylospora chaetoclada Ranzoni

Flagellospora penicillioides Ingold

Triscelophorus monosporus Ingold

A.2 Mostly temperate or cold

Alatospora acuminata Ingold

Anguillospora longissima (Sacc & Syd) Ingold

Articulospora tetracladia Ingold

Lunulospora curvula Ingold

Tetracladium marchalianum de Wild.

Tricladium gracile Ingold

Tricladium splendens Ingold

Group B

Temperate or cold only

No spores of this group found.

Group C

Uncommon or limited distribution

C.1 Tropical only

No spores found

C.2 Temperate or cold only

Alatospora constricta Dyko

Lemonnieria pseudofloscula Dyko

Triscelophorus acuminatus Nawawi

It is clear that the fungi with a world-wide distribution is apparently the dominant fungi in the Apies river (Table 2), especially the fungi which are typical for the colder zones of the world. *Campylospora chaetoclada*, *Flagellospora penicillioides* and *Triscelophorus monosporus* are fungi typical of the tropical zones of the world, while *Triscelophorus acuminatus* and *Lemonnieria pseudofloscula* with a limited distribution, also occurred in the Apies river. From the results it appears that the hyphomycete composition of the Apies river occupies a transitional position between that of the colder areas and the more tropical

zones, but it must be kept in mind that the validity of Nilsson's groupings are tentative (Ranzoni, 1979).

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NOTES ON *TULBAGHIA*: 3. ON THE STATUS OF *TULBAGHIA CERNUA* AVÉ-LALL.

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ABSTRACT

Tulbaghia cernua Avé-Lall. is a legitimate name and its type specimen has been located in the Herbarium of the Komarov Botanical Institute, Leningrad. The differences between *T. alliacea* L.f. and *T. cernua* Avé-Lall. are outlined.

UITTREKSEL

NOTAS OOR *TULBAGHIA*: 3. DIE STATUS VAN *TULBAGHIA CERNUA* AVÉ-LALL.

Tulbaghia cernua Avé-Lall. is 'n wettige naam en die tipe-eksemplaar is in die Herbarium van die Komarov Botaniese Instituut, Leningrad, gevind. Die verskille tussen *T. alliacea* L.f. en *T. cernua* Avé-Lall. word geskets.

The recent publication of a revision of the genus *Tulbaghia* by Burbidge (1978) has raised the question of the legitimacy of the name *Tulbaghia cernua* Avé-Lallemant.

This name was validly published in *Indice Semin. h. Petr.* 9: Append. p. 25 [1843], 1844 by Avé-Lallemant. Shortly afterwards a more complete description, including a list of synonyms and a short discussion appeared in *Bull. Class Phys. Math. Acad. Petersb.* 3: 201-208 (1844).

The short original description was also published in *Linnaea* 18: 222 (1844).

Avé-Lallemant's description was based on living plants given to him by C. F. Ecklon (. . . bulbos a nos misit cl. Ecklon . . .) which flowered in St. Petersburg, now Leningrad, in July 1842, and on herbarium specimens one of which he had seen in Kew in 1823, and two others, apparently collected by J. F. Drège in the Cape.

In his second more complete description Avé-Lallemant cited *T. alliacea* L.f. forma α Drège and *T. ludwigiana* forma macrior according to Kunth. *Enum* 4: 483 (1843) as synonyms.

In the light of the current *International Code of Botanical Nomenclature* (1978, art. 63.1) a name is superfluous or illegitimate when accepted species are cited as synonyms. In the case of *T. cernua* Avé-Lall. this is certainly not the case and I propose that the name should be considered valid.

Accepted for publication 21st May, 1980.

In my own cytotaxonomic account of the genus *Tulbaghia* (Vosa, 1975) I noted that the type specimen of *T. cernua* was not known to have been preserved. This was based on the negative results of my enquiries on the existence of such a specimen addressed to the Curator of the Herbarium of the Komarov Botanical Institute in Leningrad and to the Academy of Sciences of the Soviet Union, over several years.

However, during my recent visit to the Komarov Botanical Institute in June and July 1979, I was able to look through the collections of African Liliaceae in the Herbarium. In one of the cupboards, in various folders and under different generic names, I discovered three specimens of *Tulbaghia cernua*, clearly labelled and obviously used by Avé-Lallemant for his description, and derived from his cultivated plants.

I propose to consider specimen No. 73.6, the most complete of the three, as the holotype of *Tulbaghia cernua* Avé-Lallemant and the other two as isotypes. Specimen No. 73.6 is illustrated in Figure 1.

Figures 2 and 3 show the full size inflorescence and the label of the specimen, respectively.

The typification of *Tulbaghia cernua* is as follows:

Tulbaghia cernua Avé-Lallemant in Indice Semin. h. Petr. 9: 25 [1843], 1844; Bull. Class. Phys. Math. Acad. Petersb. 3: 202-203 (1844); Linnaea 18: 222 (1844); Vosa in Annali Bot. (Roma) 34: 71-75 (1975). Type: 73.6 (LE!). Syn.: *T. alliacea* L.f. var. *affinis* Bak. sensu Link Enum. alt. 1: 310 (1821); *T. alliacea* L.f. forma \propto Drège sensu Kunth. Enum. 4: 483 (1843); *T. ludwigiana* Harv. forma *macrior*, Kunth. Enum. 4: 483 (1843); *T. campanulata* (N.E. Br. in Kew Bull. 175: 136 (1901). Type: Cape, Queenstown Div., Mts. near Queenstown, Galpin 1660 (K!).

Icon.: Wild Flowers of the E. Cape Province by Batten and Bokelmann, Pl. 6, fig. 7 (1966) as *T. alliacea* L.f.; Vosa in Annali Bot. (Roma) 34: 75-76 (1975).

DIFFERENCES BETWEEN *T. ALLIACEA* L.f. AND *T. CERNUA* AVÉ-LALL.

Distribution

T. alliacea L.f. is found only in a restricted area in the winter rainfall region of the Cape, whilst *T. cernua* Avé-Lall. is found exclusively in the summer rainfall region on the Eastern Cape, Transkei and Natal where diploids and tetraploids are found and the Transvaal Drakensberg, where only tetraploid forms have been found so far.



Ex herbario bot. Petropoliensis. 73.6
Tulbaghia cernua A. Vell.
 Herb. 1844

FIG. 1.

The type specimen of *Tulbaghia cernua* Avé-Lall. No. 73.6, present in the Herbarium of the Komarov Botanical Institute, Leningrad (LE).

Ex horto bot. Petropolitano. 73. 6
Tilbaghia cernua Lall.
terre d'Arg.

2

FIG. 2.

The label of the type specimen of *T. cernua* Avé-Lall. reproduced natural size.



3

FIG. 3.

The inflorescence of the type specimen of *T. cernua* Avé-Lall. reproduced natural size.

Morphology

	<i>T. alliacea</i>	<i>T. cernua</i>
<i>perianth segments</i>	channel-shaped, rather thin and convolute, almost spatulate at the apex, slightly reflexed or not at all.	deltoid, acute, usually reflexed.
<i>corona</i>	fleshy, cylindrical or slightly funnel-shaped, shallowly trilobed with the lobes cleft at the apex.	fleshy, urceolate, triangular in section with round or somewhat flat corners, forming a Y-shaped slit at the apex.

Tulbaghia alliacea L.f. has always a strong alliaceous smell but most plants of *T. cernua* Avé-Lall. are inodorous or have only a slight smell.

Cytology

The two species also differ in chromosome morphology: the karyotype of *T. alliacea* belongs to Group 1 (Vosa, 1975), where the nucleolar attachment is distally located on the short arm of chromosome 2; the karyotype of *T. cernua* belongs to Group 2 (Vosa, l.c.), where the nucleolar attachment is located in an interstitial position on chromosome 6. The basic chromosome number is $n = 6$ for both species.

ACKNOWLEDGEMENTS

I wish to thank Prof. Armen Takhtajan, Director of the Komarov Botanical Institute, Leningrad, and his staff for kindness and for the use of facilities in the Institute, and Mr Frank White, Curator of the Fielding Druce Herbarium, Oxford, for helpful discussions.

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STUDIES IN THE GENERA OF THE *DIOSMEAE* (RUTACEAE):

9. A REVISION OF THE GENUS *COLEONEMA*

ION WILLIAMS

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ABSTRACT

The eight species belonging to the genus *Coleonema* Bartl. & Wendl., including one new species, are described, with keys. The lectotypes of *Diosma rubra* L. and *Diosma ericoides* L. are chosen.

UITTREKSEL

STUDIES IN DIE GENERA VAN DIE *DIOSMEAE* (RUTACEAE): 9. 'N HERSIENING VAN DIE GENUS *COLEONEMA*

Die agt *Coleonema* Bartl. & Wendl. soorte, wat 'n nuwe soort insluit, word beskryf. Sleutels word gegee. Die lektotipes vir *Diosma rubra* L. en *Diosma ericoides* L. word aangewys.

AIM AND SCOPE OF THIS WORK

The last revision of the genus *Coleonema* by W. Sonder, was published in the *Flora Capensis* in 1860. In this work Sonder recognised only four species. Since then many more collections have been made and our knowledge of the species and of their distribution ranges has vastly expanded. It is now possible to obtain an overall picture of the genus and of the geographical distribution of the species. As it seems fairly unlikely that any new species of *Coleonema* remain to be discovered, this revision is now published as part of a continuing series of studies in the *Diosmeae*.

HISTORICAL BACKGROUND

Bartling & Wendland in their revision of the *Diosmeae* (1824) proposed the generic name *Coleonema*. At that time they were acquainted with only one species (*Diosma alba* Thunb.) which they transferred to *Coleonema*. They indicated that the name was made up from two Greek words meaning sheath and filament: *Nomen compositum e choleos, vagina, et nema, filamentum, qua filamenta in petalorum canaliculum ita immersa sunt, ut in vaginis occulta diceres*.

A. du Jussieu in his *Memoir* on the Rutaceae (1825) drew attention to the fact that he was acquainted with three species of *Coleonoema* but failed to publish any valid description or combination.

Accepted for publication 3rd July, 1980.

Sprengel did not agree with Bartling and Wendland's creation of new genera in the *Diosmeae* and so in his *Systema Vegetabilium* (1825) he transferred them all back into *Diosma* resulting in a certain amount of confusion. For example Sprengel's *Diosma juniperina* was derived from *Acmadenia juniperina* and had nothing whatever to do with any species of *Coleonema* although Sonder thought it did when he proposed the name *Coleonema juniperinum* in his revision for the *Flora Capensis* (1860).

Von Schlechtendal in *Linnaea* (1831), working on Ecklon's collections, named two species of *Coleonema* merely regarding them as varieties of *C. album*.

In 1834, in *Curtis's Botanical Magazine*, an illustration of a beautiful pink flowered *Coleonema* appeared which had been in cultivation for some time in the Glasgow Botanic Garden. Named *Coleonema pulchrum* Hook. it has been, up to now, confused with three other pink flowered species of *Coleonema*.

Ecklon & Zeyher in their *Enumeratio Plantarum* (1835) mentioned six species of *Coleonema*, five of which were good species but for various reasons their name remains attached to only one.

Drège, who collected many species in the *Diosmeae*, collected very few *Colenomemas*, all of which were misidentified as *Diosma*.

As mentioned above the genus was revised by W. Sonder in the *Flora Capensis* (1860) and subsequently only one new species was described, that by Schlechter in 1899. Unfortunately he chose a name already published for another species thus making it illegitimate. The position was rectified by the substitution of the epithet *nubigenum* by Miss E. Esterhuysen in the *Journal of South African Botany* (1943).

MATERIAL AND METHODS

All descriptions, except for *C. virgatum*, have been done from fresh material collected by the author and populations have been studied in the field. Dissections have been done with the help of a Zeiss Stereomicroscope II and drawings made to scale without the aid of a drawing tube. Photographs giving a magnification of about $\times 10$ were taken with a Pentax 35 mm camera through a photographic tube using the same microscope. Pollen was examined using a Reichert microscope with an oil immersion lens and measurements taken using a graticule in the eye piece. Drawings are two dimensional only and purely diagrammatic, petals for instance being shown as flattened out. Each species description terminates with a diagnosis stating how it differs from those it most resembles.

Coleonema Bartl. and Wendl. *Diosmeae* in Beitr. Bot. 1: 55 (1824); A. Juss. in Mém. Mus. Hist. Nat., Paris 13: 471 (1825); Don Gard. and Bot. 1: 783 (1831); Curtis's bot. Mag. t.3340 (1834); Eckl. and Zeyh. Enum. Plant.: 106 (1835); Endl. Gen. Plant. 2: 1157 (1840); Lindl. Veg. Kingd.: 471 (1853); Sond.

in Flor. Cap. 1: 377 (1860); Benth. and Hook. Gen. Plant. 1: 289 (1862–1867); Engl. Pflanzenfam. 19a: 272 (1931); Dyer Gen. S. Afr. Flow. Pl. 1: 290 (1975). Type species: *C. album* (Thunb.) Bartl. & Wendl. (*Diosma alba* Thunberg).

Diosma L. Sp. Pl. 1: 198 (1753).

Adenandra Roem. & Sch. Syst. Veg. 5: 451 (1819).

GENERIC DESCRIPTION

Shrubs 0.3–2.7 m tall, virgate, erect, arising except for *C. nubigenum*, from a single stem at base. *Branchlets* numerous, erect, fairly slender, glabrous, puberulous or thinly villous. *Leaves* 5–35 mm long, 0.7–1.5 mm broad, linear or linear-lanceolate, acute, mucronate, petiolate, alternate, glabrous, gland-dotted \pm in two rows; margins narrowly translucent, smooth, ciliolate, serrulate or villous-ciliate. *Flowers* solitary, terminal or axillary, subtended by two bracteoles and 3–8 bracts (reduced leaves). *Petals* five, spreading, white or pink; *claw*, except for *C. nubigenum*, connate with the staminode. *Anthers* five, each with a minute apical gland. *Pollen* 33–47 μ long, 18–30 μ broad, ellipsoid, tri-porate. *Disc* obvallate, narrow, partly free, fairly level on top. *Stigma* 0.2–0.65 mm diam., capitate, depressed globose. *Style* and *filaments* short, glabrous. *Ovary* 5-carpellate, glabrous; apices globose with an immersed gland. *Fruit* 5-carpellate, glabrous, hornless or with horns short, spreading or erect.

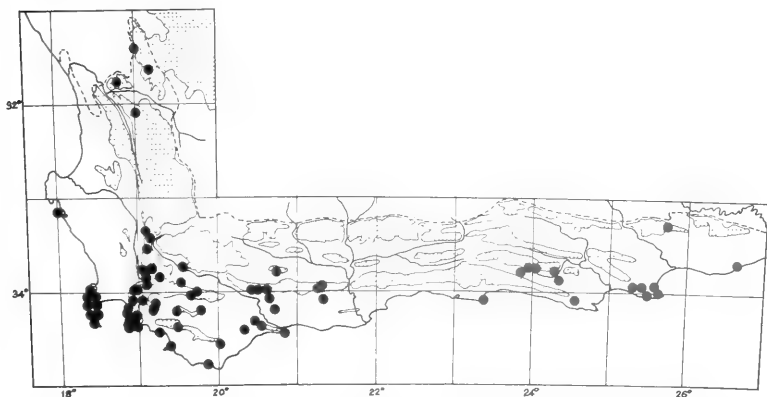


FIG. 1.

Distribution of the genus *Coleonema*. Dashed line shows boundary of the Cape Geological Series. Dotted areas show elevated ground.

DISTRIBUTION

Eight species of *Coleonema* are found in the south-western and southern Cape Province, extending from the Cape Peninsula northwards to Nieuwoudt-

ville and eastwards to the mouth of the Bushmans River, all within an area defined by the Cape Geological Series, the northern boundary of which is indicated by a line of dashes on the distribution maps.

KEY TO THE SPECIES OF *COLEONEMA*

- 1 Staminode not connate with the petal **nubigenum** 1.
- 1⁺ Staminode partly connate with the petal 2
- 2 Flowers white, * petals up to 5 mm long 3
- 2⁺ Flowers usually pink, petals over 5 mm long 5
- *Note: Buds may sometimes be tinged with pink but flowers are white when open.
- 3 Flowers 3–4 mm diam., petals papillose **juniperinum** 2.
- 3⁺ Flowers more than 5 mm diam., petals smooth 4
- 4 Leaves 13–19 mm long, 0.7–1 mm broad, flowers 5.5–6.5 mm diam. **calycinum** 3.
- 4⁺ Leaves 12–13.5 mm long, 1.3–1.5 mm broad, flowers 6–7 mm diam. **album** 4.
- 5 Petals tapering evenly to the base **aspalathoides** 5.
- 5⁺ Petals with a narrow claw 6
- 6 Leaves 8–10 mm long, petals 5–5.7 mm long **pulchellum** 6.
- 6⁺ Leaves 15–35 mm long, petals 6.3–8.5 mm long 7
- 7 Petals 6.3–6.5 mm long, eglandular **virgatum** 7.
- 7⁺ Petals, 7.6–8.5 mm long, gland-dotted **pulchrum** 8.

1. *Coleonema nubigenum* Esterhuysen in Jl S. Afr. Bot. 9: 137 (1943). Type: In regione austro-occidentali: In clivis montium prope French Hoek, alt. c. 3 000 ped., 18/11/1896, *Schlechter* 9299 (BOL, lectotype; BM, G, GRA, PH, PRE, S, isotypes).

Coleonema gracile Schltr. in Bot. Jb. 27: 163 (1899) nom. illegit. Non *C. gracile* Eckl. & Zeyh. Enum. Plant. 1: 106 (1835).

Shrubs to 1 m tall, dense, rounded with many stems arising from a single rootstock, apparently able to coppice. *Branches* numerous, erect, glabrous, stout, tough, more or less clustered; bark dark brown, rough with circumferential leaf scars. *Branchlets* numerous, erect, slender, thinly deflexed, villous, green, clustered. *Leaves* 5–9 mm long (including the petiole 1–1.3 mm long), 1–1.3 mm broad, narrowly lanceolate, somewhat obtuse with a blunt callus at the apex, glabrous, recurved-erect, alternate; margins narrowly translucent, at first villous-ciliate becoming eciliate; abaxial surface rounded, gland-dotted to either side of the mid-rib and along both margins. *Inflorescence* solitary, terminal or axillary, subtended by two or three reduced leaves, one bract and two bracteoles; *flower* 7.5 mm diam. with petals white, soon delapsing. *Bract* 2 mm long, 0.6 mm broad, linear-lanceolate, narrowed above; apex with a red callus; margins densely crisped ciliate; adaxially densely crisped pubescent; abaxially glabrous and gland-dotted above, somewhat pubescent below. *Bracteoles* two, 1.5 mm long, 0.6 mm broad, lanceolate, obtuse; apex with a blunt callus; margins crisped ciliate, translucent below; adaxially somewhat pubescent; abaxially rounded, gland-dotted above, pubescent below. *Calyx lobes* five, 1.7 mm long, 1.1 mm broad, elliptic, glabrous, ciliate, translucent, apex minutely callused,

gland-dotted on the midrib above. *Petals* five, 3,6–5 mm long overall, 1,9–2,9 mm broad, orbicular with the apex truncate or emarginate, white, glabrous, faintly veined, gland-dotted to either side of the midrib; *claw* about 2 mm long narrowing to the base. *Staminodes* five, 1–1,3 mm long, 0,3–0,4 mm broad, fusiform, narrowed below, apex gland tipped, glabrous. *Filaments* five, becoming 1 mm long, somewhat fusiform, glabrous. *Anthers* five, 0,7–1 mm long, 0,6 mm broad, yellow; apical gland globose, incurved, minutely stipitate. *Pollen* 38–40 μ long, 18–20 μ broad, ellipsoid. *Disc* obvallate, slender, exceeded by the ovary, hidden from above by the swollen filaments and staminodes. *Stigma* 0,2 mm diam., capitate. *Style* glabrous, slender, deflexed at first, becoming erect, 1 mm long. *Ovary* 5-carpellate, 0,7 mm diam., glabrous, lumpy with oil glands. *Fruit* 5-carpellate, 5 mm long, 5 mm diam., glabrous, gland-dotted, green, purplish above, deeply divided, hornless, apices emarginate. *Seed* 3,5–4,1 mm long, 1,7 mm broad, black, shining; aril black.

This species from the mountains of the South Western Cape Province was apparently first collected by Oldenburg when at the Cape in 1772. It remained virtually unnoticed however until collected by Schlechter in 1896. Unfortunately, in describing the plant, he chose the epithet *gracile* a name which had already been used by Ecklon & Zeyher for another quite different species in the same genus. Miss E. Esterhuysen of the Bolus Herbarium therefore renamed the species *Coleonema nubigena*. Schlechter distributed duplicates to many herbaria. But as was usual he did not nominate the holotype and so, in view of this, Schlechter's specimen at the Bolus Herbarium has been chosen as the lectotype. The epithet *nubigena* is perhaps more correctly spelt *nubigenum* in order to agree in gender with the generic name which is neuter.

SPECIMENS EXAMINED

CAPE—3318 (Cape Town): Jonkershoek, Stellenbosch Division (-DD), 17/11/1935, *Berg s.n.* (BOL); Jonkershoek valley, rocky slopes, W. aspect, along path below cliffs, Stellenbosch Division, 2 500–3 000 ft., 12/11/1961, *Esterhuysen 29294* (BOL); Banhoek Valley, slopes of Drakenstein Mountains, Stellenbosch Division, -/12/1939, *Esterhuysen 1469* (BOL, PRE).

—3319 (Worcester): French Hoek, Paarl Division (-CC), 3 300 ft., 19/11/1896, *Schlechter 9299* (BM, BOL, G, GRA, PH, PRE, S), 3 600 ft., 20/12/1895, *H. Bolus s.n.* (NBG); French Hoek Forest Reserve, Paarl Division, 28/9/1935, *Compton 5781* (NBG); Haalhoek Sneeuwkop, S.E. slopes, Paarl Division, 3 000 ft., -/12/1938, *Esterhuysen 1224* (BOL); S. slopes of Tierkloof, Wemmershoek, Paarl Division, 3 000–4 000 ft., 5/11/1950, *Esterhuysen 17729* (BOL, PRE); Wemmershoek valley, Paarl Division, -/12/1944, *Stokoe s.n.* (SAM); Du Toits Peak, frontal ridge, Worcester Division, 28/2/1960, *Esterhuysen 28451* (BOL).

—3418 (Simonstown): Somersetsneeuwkop, slopes above Diepgat, Caledon

Division (-BB), 4 000 ft., 13/12/1942, *Esterhuysen 8246* (BOL); Somersetsneeuwkop, on S.E. slopes, Caledon Division, 4 000 ft., -/12/1939, *Esterhuysen 4268* (BOL, NBG, PRE); Somersetsneeuwkop, Caledon Division, 3 750 ft., -/2/1943, *Stokoe s.n.* (SAM); Somersetsneeuwkop/Landdrostkop, Caledon Division, 26/9/1943, *Stokoe 9278* (NBG, 8862 at PRE); above zigzag on path to Somersetsneeuwkop, Caledon Division, 18/12/1971, *Vogelpoel W. 1610* (NBG, PRE); on zigzag path to Somersetsneeuwkop, Caledon Division, 4 350 ft., 28/12/1975, *Williams 2168* (NBG); Landdrostkop, Caledon Division, 3 000 ft., -/12/1940, *Stokoe 7669* (NBG, PRE, SAM); Landdrostkop, N. side near path, 3 900 ft., 28/12/1975, *Williams 2166* (NBG).

—3419 (Caledon): Victoria Peak, S. slopes, Caledon Division (-AA), 4 000 ft., 2/1/1944, *Esterhuysen 9755* (BOL, PRE); between Viljoens Pass and Somersetsneeuwkop, Caledon Division, -/10/1938, *Stokoe 6523* (BOL); Nuweberg Forest Reserve near end of road to hut, Caledon Division, 3 400 ft., 28/12/1975, *Williams 2173* (NBG); S.E. slopes of Rooskraalberg, Caledon Division, 3 000 ft., -/7/1940, *Esterhuysen 2645* (BOL); Dwarsberg, Jonkershoek, Stellenbosch Division, 9/2/1959, *Rycroft 2141* (NBG); W. edge of Dwarsberg, Jonkershoek, zigzag beyond 2nd waterfall, Stellenbosch Division, 3 200 ft., 30/1/1963, *Taylor 4619* (PRE, STE), 4 000 ft., 13/3/1967, *Kruger 407* (PRE), 3 800 ft., 12/11/1965, *Taylor 6586* (PRE).

Without locality: -/1772, *Oldenburg 1281* (BM), *Niven s.n.* (BM).

DISTRIBUTION AND BIOLOGY

Coleonema nubigenum is endemic to the Hottentots Holland, French Hoek and Du Toits Kloof Mountains. This is a fairly narrow area less than 40 km in length from north to south, enjoying what is probably the highest rainfall in the country. The plants are found at altitudes of between 900 and 1 400 m above sea level. Flowering has been observed to begin in September, with plants in full bloom from November to February. Specimens with ripe fruits have been collected from December to March. The plants are tough with many stems and appear to coppice from the stump. The small white flowers stand wide open with the narrow disc hidden beneath fusiform staminodes and filaments. Although the presence of nectar has not been observed, the pollen does not appear to be dispersed by wind so one may conclude that the flowers are pollinated by insects. Seed when ripe is dispersed by the usual catapult mechanism. The leaves when crushed have a pleasant smell rather like coconut.

Neither variation nor hybridisation have been observed.

DISCUSSION

Of this plant, in the genus *Coleonema*, Schlechter remarked "The above plants can be recognised from all other species in the genus by their staminodes

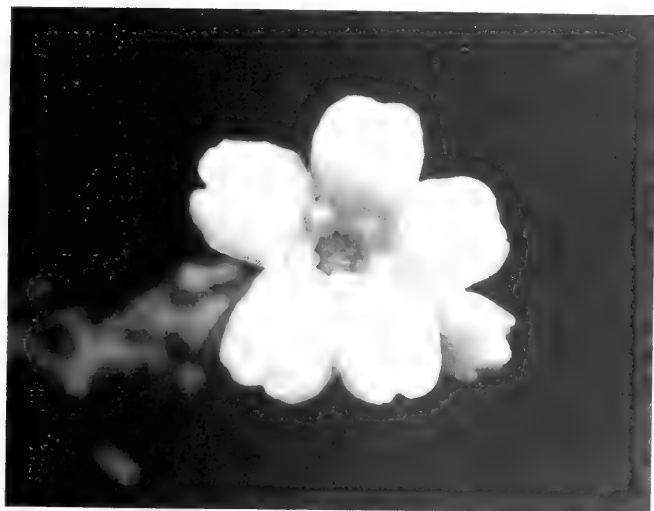


FIG. 2.
Coleonema nubigenum: flower, 7,5 mm diam.

which are quite free of the petals and by the blunt, mostly visibly separated and distinct petals. In appearance they are mostly like *C. juniperinum* Sond., . . .” In support of Schlechter’s decision to place this species in *Coleonema*, in spite of its not possessing the one character most typical of the genus, viz. that of having the staminodes connate with the petal, one takes into account the following characters that are typical of other plants in the genus: the numerous branchlets; the narrow, alternate leaves; the occasionally axillary and solitary flowers; the numerous modified leaves at the base of the flower; the very open throat of the flower (compare with *C. calycinum* in Fig. 6); the staminode although not lying in a groove in or connate with the petal, actually arises close to the base of the petal, its fusiform shape compares well with that of the staminode in *C. juniperinum* (Fig. 5 No. 6); the narrow obvallate disc is typical of that in all species of *Coleonema* and is also exceeded by the ovary in both *C. album* and *C. juniperinum*; the 5-carpellate fruit; the sweet smell of the leaves when crushed.

Coleonema nubigenum is a very distinct species. It differs from all others in the genus in having: (1) a tendency to coppice from the root; (2) leaves with a blunt point; (3) staminodes not connate with the petals; (4) style at first deflexed; (5) stigma very much smaller; (6) fruits without horns.

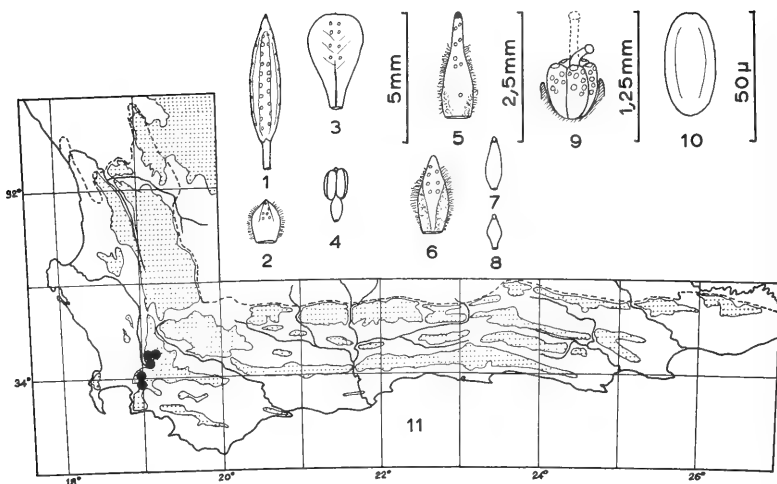


FIG. 3.

Coleonema nubigenum: 1, leaf. 2, calyx lobe. 3, petal. 4, anther. 5, bract. 6, bracteole. 7 and 8, staminodes. 9, gynoecium and disc. 10, pollen. 11, distribution.

2. *Coleonema juniperinum* Sonder in Fl. Cap. 1: (1860). Type: Kleinhouwhoek, Caledon Division, Zeyher 2150 (S, lectotype; SAM, isolectotype).

Coleonema juniperifolium Eckl. & Zeyh., Enum. Plant.: 106 (1835), nom. nud. Type: In lateribus montium Hottentotshollands et Hauhoeksberge (Stellenbosch). Ad montes Zwarteberg et Kleinriviersberge (Caledon). Aug. Sept. *E. & Z.* 834 (C, G, S, SAM).

Coleonema virginianum Eckl. & Zeyh., Enum. Plant.: 106 (1835), nom. nud. Based on: Inter saxa (altit. IV) laterum montium prope Tulbagh (Worcester). Nov. *E. & Z.* 835 (C, G, PRE, S, SAM, etc.). Non *Diosma juniperina* (Bartl. & Wendl.) Spreng. Syst. Veg. 1: 784 (1825) = *Acmadenia juniperina* Bartl. & Wendl.

Shrubs 0.3–0.5 m tall, dense or if amongst other vegetation diffuse and sprawling, single-stemmed at base. *Branches* slender, tending to sprawl, variously bent, glabrous, smooth, longitudinally slightly wrinkled, reddish-brown. *Branchlets* numerous, extremely slender, virtually glabrous (most minutely puberulous at first), bright red, alternate. *Leaves* 5–7 mm long, 0.8 mm broad, linear-lanceolate, acute, mucronulate, glabrous, petiolate, alternate, adpressed erect, imbricate at first; hyaline margins thin, subserrulate, extremely narrow; abaxial surface convex with many gland-dots in two rows; adaxial surface flat when fresh. *Inflorescence* solitary, terminal or axillary towards the apices of the branchlets, about 3 mm diam., white. *Basal bracts* \pm four, 0.6–0.7 mm long, 0.3–0.5 mm

broad, lanceolate to ovate, mucronulate, ciliolate with broad translucent margins, glabrous; adaxially pubescent above. *Bracteoles* two, 0,8 mm long, 0,6 mm broad, elliptic, obtuse, ciliolate with broad translucent margins, glabrous, sacculate; midrib one or two gland-dotted, apex gibbous. *Calyx lobes* five, 1,1 mm long, 0,8 mm broad, oblong, obtuse; apex elevated, obtuse, reddened; margins ciliolate, broadly translucent; adaxial surface pubescent; abaxial surface glabrous, gland-dotted. *Petals* five, 2 mm long, 1,1 mm broad above narrowing evenly to the base, obovate, obtuse, minutely apiculate, glabrous; *blade* pappilose adaxially, sometimes pink-tipped outside; *claw* connate with the staminode below with a short elevated groove almost embracing the tip of the staminode and fitting neatly into the lateral grooves of the anthers before anthesis. *Staminodes* five, 0,7 mm long, fusiform, acute, glabrous. *Filaments* five, becoming 1,2 mm long, glabrous, acicular, elevating each anther in turn from between the petal ridges into the centre of the flower. *Anthers* five, 0,6 mm long, 0,4 mm broad, yellow; apical gland minute, sessile, globose. *Pollen* very variable, up to 33 μ long, 18 μ broad, elliptical with rather pointed ends. *Disc* obvallate, narrow, 5-lobed, green, exceeded by the ovary, nectariferous. *Stigma* 0,2 mm diam., capitellate. *Style* becoming 0,5 mm long, glabrous, erect. *Ovary* 5-carpellate, 0,6 mm long, 0,5 mm diam., glabrous, apices obtuse. *Fruit* 5-carpellate, 4,5 mm long, 4 mm diam.; *carpels* glabrous, multi-gland-dotted, reddened, strongly veined when dry; *horns* 0,5 mm long, spreading. *Seed* 3,1–3,3 mm long, 1,3–1,4 mm broad, black, shining; aril black.

Sonder, in describing *Coleonema juniperinum*, cites specimens collected by Ecklon and Zeyher from the mountains of the Hottentotsholland, Houhoek, Caledon Swartberg and Kleinrivier and from near Tulbagh. In particular he cites Zeyher 2150 from Houhoek as being partly *C. juniperinum* and partly his var. β , a variety which appears to be indistinguishable from the original species. This sheet housed at Stockholm bears a label in Sonder's handwriting with the inscription "2150 Coleonema juniperinum Sdr., Klynhouhoek, Decbr., Zeyher". It consists of three twigs 250–340 mm long at the early fruiting stage and has been selected as the lectotype. Another sheet which Sonder undoubtedly examined has the very dubious locality "Table Mountain near Constantia". This consists of specimens in the flowering stage in good condition and bears a capsule containing portions of a flower with a description in Sonder's handwriting. The source from which Sonder appears to have derived his epithet *juniperinum*, "Diosma juniperina Spreng, Herb. Zey. 397" is a misidentification, Sprengel having made the new combination *D. juniperina* when he transferred all Bartling and Wendland's genera including *Acmadenia* back to *Diosma*. It should be noted that Drège's labels marked "Diosma virgata C. F. W. Meyer" are attached to the specimens of *C. juniperinum*.

SELECTED SPECIMENS EXAMINED

CAPE—3319 (Calvinia): Van Rhyns Pass summit, Vanrhynsdorp/Calvinia Division (-AC), 2 200 ft., 23/8/1972, *Williams 1676* (NBG, PRE); Lokenberg ridges W. of Themeda Valley, 2 m tall, Calvinia Division (-CA), 2 300 ft., 24/9/1955, *Leistner 418* (NBG, PRE).

—3318 (Vanrhynsdorp): Gifberg, 3–4 ft. tall, Vanrhynsdorp Division (-DD), 1–2 000 ft., 13/9/1911, *Phillips 7535* (BOL, PRE, SAM).

—3219 (Clanwilliam): Pakhuis Pass, along path to Heuning Vlei, 2–3 ft. tall, Clanwilliam Division (-AA), 2–3 000 ft., 29/9/1940, *Esterhuysen 3139* (BOL, NBG, PRE).

—3319 (Worcester): Inter saxa (altit. IV) laterum montium prope Tulbagh (-AC), -/11/-, *E. & Z. 835* (C, G, PRE, SAM), *Zeyher 77.11* (C, E, GRA); Summit of Pass above Kluitjieskraal, 0.25 m tall; Tulbagh Division, 2 000 ft., 8/11/1974, *Williams 1926* (NBG); Bainskloof, Worcester Division (-CA), 3 700 ft., 14/11/1874, *Schlechter 9185* (BM, GRA, PRE); Dutoitskloofberg (-CA or -CD), 4 000 ft., 30/11/1827, *Drège III. A.e.* (BOL, BM, E, G, P); French Hoek, Paarl Division (-CC), 1 000 ft., 6/10/1964, *Compton 18555* (NBG); Stettynskloof, Worcester Division (-CD), 19/8/1961, *Barker 9466* (NBG); Jonaskop, at end of side road to stream, Worcester Division, 2 800 ft., 19/10/1971, *Williams 1561* (NBG, PRE); Scherpenheuvel, hillside, Worcester Division (-DA), 29/9/1951, *Barker 7525* (NBG); Jonaskop, N. slopes, Worcester Division (-DC), 4 500 ft., 25/9/1965, *Rycroft 2884* (NBG).

—3318 (Cape Town): Banhoek Valley, slopes of Drakenstein Mountains, Stellenbosch Division (-DD), -/12/1939, *Esterhuysen 1375* (BOL, NBG, GRA, PRE).

—3418 (Simonstown): Upper Lourens River Valley, Somerset West Division (-BB), 600 m, 30/10/1945, *Parker 4007* (NBG, PRE); In saxosis pr. Sir Lowrys Pass, Somerset West Division, 400 ft., 15/7/1892, *Schlechter 1110* (BM, G, GRA); Kogelberg, Caledon Division, 2 000 ft., 16/11/1944, *Compton 16453* (BOL, NBG); Hangklip, Caledon Division, 18/11/1944, *Compton 16499* (NBG).

—3419 (Caledon): Nieuweberg, Caledon Division (-AA), 2 500 ft., 26/8/1940, *Bond 498* (NBG, PRE); Groenlandberg, N. side, Caledon Division, 2 200 ft., 31/5/1973, *Williams 1811* (NBG); Kleinhouhoek, Caledon Division, *Zeyher 2150* (S, SAM); In rupestris mtis. Zwartberg pone Caledon (-AB), 1 000 ft., -/10/1886, *MacOwan H.N.A.A. 710* (BM, E, G, PRE, SAM); Zwartberg und Umgegend des Bades, Caledon, 1 000–2 000 ft., -/11/-, *Zeyher 3775* (E, G, S, SAM); Honingklip, Bot River, Caledon Division (-AC), 19/11/1955, *Taylor 4581* (NBG, PRE); Kleinrivier Mountains, Caledon Division, (-AD?), *Stokoe 7093* (PRE); 51.11, -/11/-, *Zeyher 3775* (E, G, S, SAM); Galgeberg/Bushmanskloof Pass, Robertson Division (-BA), 2 800 ft., 23/3/1972, *Williams 1631* (NBG, PRE, S), 24/9/1941, *Walgate 344* (NBG, PRE); Bei Genadendal, 2 500/3 500 ft., 28/10/1828, *Drège IV A* (G, P, S, SAM).

Without definite locality: In lateribus montium Hottentots-hollands et Houhoeksberge (Stellenbosch). Ad montes Zwartberg et Kleinriviersberge (Caledon). Aug. Sept. Ecklon & Zeyher 834 (C, G, S, SAM), Thunberg 5708 (UPS), Masson s.n. (BM, G), Niven 64 (BM), Roxburgh s.n. (BM), Verreaux s.n. (BM, G).

With locality doubtful: Elim, 300 ft., 25/4/1896, Schlechter 7733 (BM, E, G, GRA, PRE, PH, S).

DISTRIBUTION, VARIATION AND BIOLOGY

C. juniperinum is mainly found in the Caledon and Worcester divisions and concentrates towards the south western corner of this area. There is an extraordinary disjunction towards the north, a distance of about 130 kilometres, before the species reappears between Clanwilliam and Nieuwoudtville in a much more arid environment. No variation in the floral parts has been observed but plants from the northern populations appear to be more rigid, rather prickly, and taller, while the leaves tend to be more spreading. Within the Kogelberg area at the south western corner of the Caledon division, plants have been found with leaves that are more obtuse at the apex (*Compton 16453*).

The small open flowers with sticky pollen and the disc exuding nectar are undoubtedly pollinated by insects. Although the plants may produce many stems at the surface of the ground, they do not appear to coppice after fires and so regeneration can only take place from seed which is ejected in the usual way by a catapult mechanism when ripe. Buds start forming in April and May with flowering continuing until November. Fruiting appears to last from September until March. The leaves when crushed have a faint resinous smell of pine or cedar.

DISCUSSION

The following characters serve to place this species in the genus *Coleonema*; at the same time they exclude it from any other genus of the *Diosmeae*: (1) *flowers* solitary, terminal or axillary, each with several basal bracts; (2) *petal* with an elevated groove enclosing the apex of the staminode, connate with the staminode below; (3) *anther* with a minute apical gland; (4) *disc* obvallate, thinly lobed, exceeded by the ovary; (5) *stigma* capitate; (6) *style* and *filaments* short, glabrous, erect; (7) *ovary* 5-carpellate.

Coleonema juniperinum is a distinct species with small white flowers, 3–4 mm diam., the smallest in the genus; with petals papillose; with slender filiform branchlets and small leaves showing only two rows of gland dots.

3. *Coleonema calycinum* (Steud.) Williams, comb. nov.

Diosma calycina Steud. in *Flora* 34: 549 (1830). Type: Pr. bon. sp. *Ludwig* 550 (PH, lectotype).

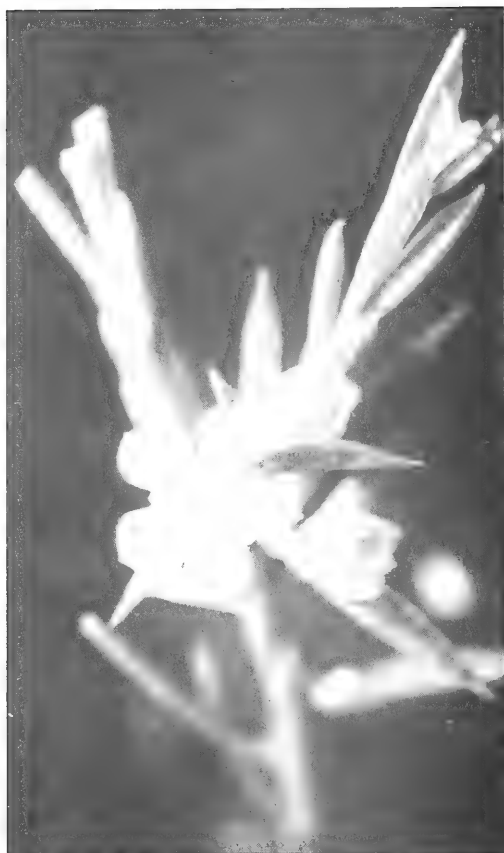


FIG. 4.

Coleonema juniperinum: flower, 3 mm diam.

Coleonema album var. *gracile* Schlechtendal in Linnaea 6: 199 (1831).

Coleonema gracile (Schlechtendal) Eckl. & Zeyh., Enum. Plant.: 106 (1835).

Type: In locis umbrosis et apertis aridolapidosiss laterum montis Baviaansberg prope Genadenthal (Caledon) Nov. Ecklon & Zeyher 833 (C, SAM).

Diosma tenuifolia Presl., Bot. Bem.: 31 (1844) nom. nud.

Diosma oppositifolia sensu Drège in Zwei pflanz. Doc.: 174, 115 (1844) in error.

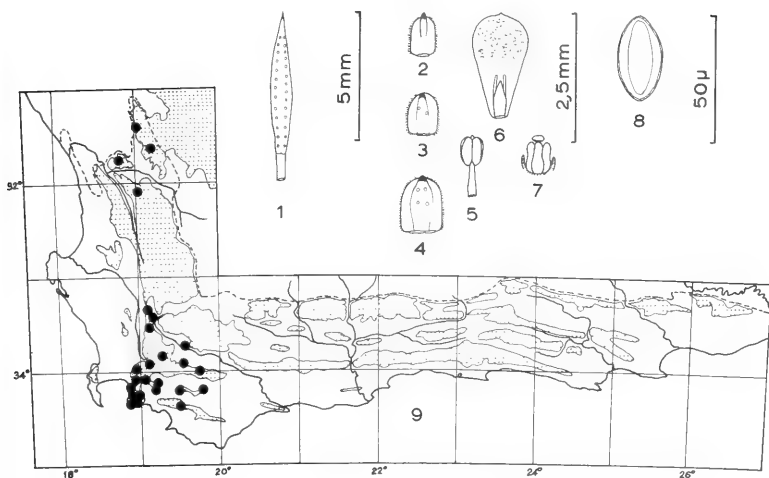


FIG. 5.

Coleonema juniperinum: 1, leaf. 2, uppermost bract. 3, bracteole. 4, calyx lobe. 5, anther. 6, petal with staminode. 7, gynoecium and disc. 8, pollen. 9, distribution.

Shrubs from (Williams 2027, 3/8/1975) 1.7–2.7 m, erect, single-stemmed at ground level, forming a large bush. *Branches* erect, numerous, glabrous, alternate; bark transversely marked with leaf scars. *Branchlets* erect, slender, numerous, alternate, minutely puberulous, not hidden by the leaves. *Leaves* 13–19 mm long, 0.7–1 mm broad, linear, acute, glabrous except up the middle of the adaxial surface where sometimes sparsely puberulous, alternate, spreading-erect; hyaline margins narrow, minutely and somewhat sparsely serrulato-ciliolate; abaxial surface convex with two rows of gland dots. *Inflorescence* solitary, terminal or axillary; buds sometimes pinkish; *flowers* 5.5–6.5 mm diam., white, standing open, pedicellate. *Bract* the uppermost of about seven adpressed scales which increase in size towards the calyx. 1.2 mm long, 0.9 mm broad, sub-deltoid, glabrous; midrib gland-dotted above with a sharp point; margins broadly translucent, ciliate. *Bracteoles* two 1.2 mm long, 0.9 mm broad, orbicular, glabrous, apex with a sharp or a rounded point; margins broadly translucent, ciliate; adaxial surface pubescent in the middle above. *Calyx lobes* five, 1.2 mm long, 1.2 mm broad, deltoid, obtuse-sacculate, with a gland at the apex, or acute with a sharp point, glabrous; margins broadly translucent, ciliate; adaxial surface pubescent towards the midrib. *Petals* five, 3.5–4.5 mm long, obovate, white, soon delapsing; *limb* 1.9–2.4 mm broad, spreading, with or without one or two hairs and gland dots; *claw* narrowing to the base, connate with the stam-

node below and with an elevated groove enfolding the upper part of the staminode. *Staminodes* five, 1,7 mm long, partly connate with the petal; apex with a small gland. *Filaments* five, 1,9 mm long, glabrous, acicular. *Anthers* five, before anthesis 0,7 mm long, 0,6 mm broad, yellow; apical gland minute, sessile, globose. Pollen 45 μ long, 22 μ broad, ellipsoid. *Disc* 10-sinuate, narrow, green, equalling the top of the stigma at first and exceeding the ovary by a long way. *Stigma* 0,3 mm diam., capitate, depressed globose. *Style* 5-carpellate, 0,8 mm diam., glabrous; carpels with globose apices. *Fruit* 5-carpellate, 4,5 mm long; carpels glabrous, multi-gland-dotted; *horns* 1 mm long or less, spreading at 45°. *Seed* (from Williams 2239, 9/11/1976) 3–3,5 mm long, 1,4–1,6 mm broad, black, shining; aril with a black skin over the apex.

The material that Steudel worked on was probably destroyed during the 1939/45 war and so the very poor fragment of Baron von Ludwig's collection, preserved in the herbarium of the Academy of Natural Sciences at Philadelphia, has been chosen as the lectotype.

It was customary for travellers, including many botanical collectors, to make the mission station at Genadendal one of their stops and as a result of this, *C. calycinum* was collected by Baron von Ludwig, by Ecklon, by Drège and others in the first half of the nineteenth century. After that it was only collected once more, about a hundred years later, by Dr K. H. Barnard of the South African Museum. Recent extensive searches have failed to discover it in this area which has been repeatedly ravaged by fires and almost completely overrun by invasive alien plant species. As a result the description above is based almost entirely upon specimens collected from Windhoek in the limestone hills near the De Hoop Vlei in the Bredasdorp Division.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Boschiesveld Mtns., Worcester side (-CD), 1/10/1955, *Stokoe s.n.* (SAM); higher slopes near trig. beacon MI-ER152 between Villiersdorp and McGregor, Worcester Division, 2 300 ft., 17/10/1973, *Taylor 8624* (STE); Ouhangsborg, above Hammanshof, Worcester Division, 2 575 ft., 18/9/1977, *Williams 2350* (NBG).

—3320 (Montagu): Kloof at base of Leeuriviersberg, Swellendam Division (-CD), 17/5/1958, *Esterhuysen 27753* (BOL, BM, BR, C, E, G, K, L, M, MO, NBG, PRE, STE), 1/9/1958 *Esterhuysen 27875* (BOL, BM, BR, C, E, G, K, L, M, MO, NBG, PRE, STE); Warmwatersberg, south side near Barrydale (-DC), 3 200 ft., 4/12/1974, *Williams 1943* (NBG).

—3419 (Caledon): in shady and open dry stony places on the slopes of the Baviaansberg mountain near Genadendal, Caledon Division (-BA), 1 000–1 500 ft., -/10/-, *Ecklon & Zeyher 833* (C, SAM); Genadendal in the Baviaanskloof and on the mountain in rocky places usually a little shady and damp, 1 000

—2 000 ft., -/10/-, *Drège IV.A.8* (BM, E, G, K, SAM); by the side of the stream in the Baviaanskloof, Genadendal, -/10/1864, *Prior s.n.* (K); Genadendal, -/-/1854, *Roser s.n.* (PRE), *Barnard s.n.* (SAM); Houhoek (-AA), -/12/-, *Zeyher s.n.* (SAM).

—3420 (Bredasdorp): Kathoek, Bredasdorp Division (-AD), 300 ft., *Acocks 22754* (K, PRE); De Hoop, Bredasdorp Division, less than 200 m, -/9/1969, *v.d. Merwe 1123* (PRE); Windhoek, N. end of De Hoop vlei kloof, Bredasdorp Division, 76 m (250 ft.), 3/8/1975, *Williams 2027* (NBG), 9/11/1976, *Williams 2239* (NBG); Potberg Nature Reserve, flats on top of Potberg, Bredasdorp Division (-BC), 470 m, 18/10/1978, *Burgers 1453* (CPA Nat. Cons. Herb.).

—3321 (Ladismith): Kampscheberg, Riversdale Division (-CC), 3–4 000 ft., -/10/1926, *Thorne s.n.* (SAM 38844).



FIG. 6.
Coleonema calycinum: flower, 5,5 mm diam.

DISTRIBUTION, BIOLOGY AND VARIATION

C. calycinum is found in what appear to be isolated relict populations which are rather widely separated from each other. These are on the Warmwatersberg, the Langeberg, the Riviersonderend mountains, the Bredasdorp limestone hills and the Potberg. In most cases the plants grow on south-facing slopes at the base of rocky cliffs.

Flowering would seem to be at its height from September to October with seeds ripening in November and December. Pollination is no doubt effected by insects which are attracted in swarms to the plants. Regeneration can only take place from seed as there is no evidence of any persistent rootstock. One plant 1.7 m tall with a stem diameter of 46–52 mm showed about 24 annual growth rings. The plant gives off a pleasant smell reminiscent of bay rum.

Plants from near the Bredasdorp Division exhibit calyx lobes with the apex obtuse-sacculate, whereas those from further inland have the apices of the calyx lobes acute with a sharp point. Buds may have a pinkish tinge, particularly noticeable in the Potberg population. The type specimen and some of the material collected by Ecklon have leaves rather more widely spaced and longer than normal but this may perhaps be due to etiolation.

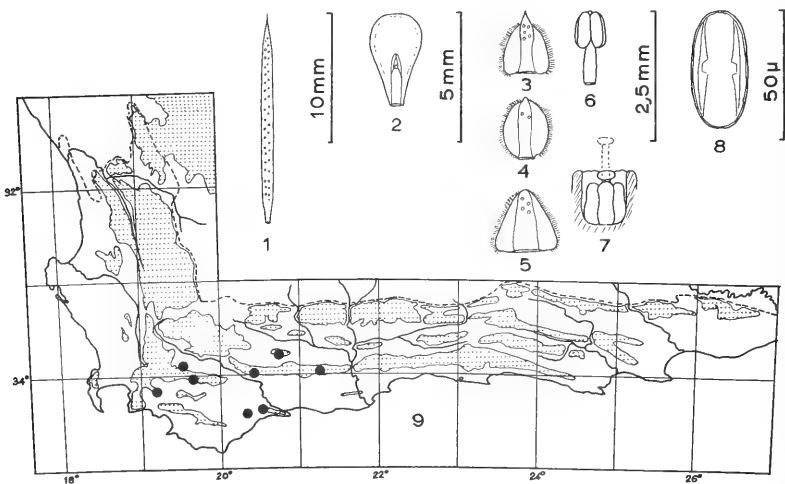


FIG. 7.

Coleonema calycinum: 1, leaf. 2, petal with staminode. 3, uppermost bract. 4, bracteole. 5, calyx lobe. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

DISCUSSION

Although plants of *C. calycinum* may be found with pink buds, the flowers appear white when open. It is distinguished by having: (1) leaves 13–19 mm

long; (2) *calyx lobes* 1,2 mm long; (3) *petals* obtuse and *staminodes* connate with the petal in the lower half.

4. *Coleonema album* (Thunb.) Bartl. & Wendl., *Diosmeae* in *Beitr. Bot.* 1: 56 (1824).

Diosma alba Thunb., *Prodr. Plant. Cap.* 1: 84 (1794); *Diss. Diosm.*: 376 (1797); *Flor. Cap.* 2: 126 (1818); *Flor. Cap. ed. Schult.*: 221 (1823). Type: *Diosma alba* α , e. Cap. b. Spei, *Thunberg* (UPS-THUNB. 5657, holotype).

Adenandra alba Roem. & Schult., *Syst. Veg.* 5: 452 (1819).

Diosma rubra L. *Sp. Pl.* 1: 198 (1753) ex parte, as to L. hand spec. on sheet 240/4 in herb. Linn.

Diosma rubra L. sensu Berg. *Plant. Cap.*: 62 (1767) exclus. *syns. nom. superfl.*

Coleonema rubrum (L.) Druce in *Rep. botl. Soc. Exch. Club Br. Isl.* 1916: 616 (1917)

Diosma ericoides L. *Sp. Pl.* 1: 198 (1753) ex parte as to *syn.* Ray?; Ait. *Hort. Kew.* 1: 275 (1789); Roem. & Schult. *Syst. Veg.* 5: 455 (1819) ex parte; Sims in *Curtis's Bot. Mag.* 2322 (1822).

Diosma juniperifolia Salisb. *Chap. All.*: 142 (1769), *nom. superfl.* Type: as for *Diosma rubra* L.

Icones: Mill. *Gard. Dict. Fig. Plant.* t.124, f.2 (1756); Sims in *Curtis's Bot. Mag.* 49. f.2332 (1822); Bartl. & Wendl. in *Beitr. Bot.* 1. t.A, f.3 (1824); Juss. in *Mém. Mus. Hist. Nat., Paris* 13. t.19, f.17 (1825); Ballion *Hist. Pl.* 4: 383, 384 (1873); Engl. *Pflanzenfam.* 3. 4. f.126, A-K (1896); Kidd, *Wild Fl. Cap. Pen.* pl. 43, f.4 (1950); Mason, W. *Cape Sandveld Flow. pl.* 60, f.7 (1972).

Shrubs to 1 m tall, dense, branching from the base. *Branches* spreading, variously bent, glabrous; *bark* greyish-brown, rough with horizontal leaf scars. *Branchlets* fairly numerous, erect, slender, densely puberulous, purplish, not hidden by the leaves except near the tips of new shoots, bark soon splitting decurrent from either side at the base of each petiole. *Leaves* 12–13,5 mm long including the petiole 1 mm long, 1,3–1,5 mm broad, oblanceolate-linear, acute, sharply mucronate, alternate, spreading, sometimes slightly recurved; hyaline margins narrow, denticulate or serrulate; adaxial surface somewhat convex when fresh, minutely puberulous along the middle towards the base; abaxial surface convex, 5-striped with 2 rows of gland dots and a few more scattered towards the margins. *Inflorescence* solitary, axillary, crowded towards the apices of the branchlets, the uppermost often terminal; buds pinkish tinged; flower 6–7 mm diam. *Bracts* numerous, as many as ten counted including 2 bracteoles, much reduced, some readily delapse, more or less in pairs as to size, increasing in size towards the calyx, penultimate pair 1,5 mm long, 0,9 mm broad, broadly lanceolate, acute with a sharp mucro; adaxially puberulous; abaxial surface glabrous, gland-dotted; margins broadly translucent, ciliolate. *Bracteoles* two, the

uppermost pair of bracts are significantly the largest and may be referred to as bracteoles, 2 mm long, 1,3 mm broad, lanceolate, acute, sharply mucronate, adaxially pubescent in the middle above, abaxially glabrous, gland-dotted; margins broadly translucent, ciliate. *Calyx lobes* five, 2,5 mm long, 1,2 mm broad, oblong-lanceolate, acute with a minute sharp mucro; adaxial surface concave, puberulous in the middle above; abaxial surface glabrous, gland-dotted on the midrib towards the apex; margins broadly translucent, ciliate. *Petals* five, 4,8–5,1 mm long, *limb* 3 mm long, 1,9–2,1 mm broad, white, spreading, obovate, somewhat apiculate, glabrous; *claw* 2 mm long, narrowing evenly to the base, glabrous, with two elevated ridges up the middle of the adaxial surface about 0,4 mm apart forming a raised groove narrowing above. *Staminodes* five, 2 mm long, 0,3 mm broad, glabrous, with a minute pointed apical gland, connate with the petal except for 0,5 mm at the apex where free but lying within the groove of the petal. *Filaments* five, becoming 2,5 mm long, glabrous, acicular, erect. *Anthers* five, before anthesis 1,2 mm long, 0,7 mm broad, yellow with a minute globose apical gland. *Pollen* 47 μ long, 27 μ broad, ellipsoidal. *Disc* sinuate, closely surrounds the ovary but never exceeds it, dark green, exudes nectar. *Stigma* 0,3 mm diam., capitellate, green, at first just equalling the tips of the lobes of the ovary. *Style* becoming 1 mm long, glabrous, erect. *Ovary* 5-carpellate, 1 mm long, 0,9 mm diam., glabrous, minutely gland-dotted; apices oblong, obtuse with a large round immersed gland above facing outwards. *Fruit* 5-carpellate, 7 mm long overall, 5 mm diam., glabrous, lumpy with gland dots, midrib prominent, green lips between adjacent carpels pressed tightly together; *horns* 2 mm long curving upwards with an immersed gland at the tip. *Seed* 3–4 mm long, 1,6–1,9 mm broad, black, shining; aril black crested.

The holotype collected by Thunberg at the Cape of Good Hope is preserved in Thunberg's herbarium at Uppsala. It consists of three twigs mounted on sheet No. 5657 inscribed *Diosma alba* ∞ in Thunberg's handwriting with *e. cap. b. spei. Thunberg.* written on the back of the sheet. An adjacent sheet No. 5658 inscribed *Diosma alba* ? β . bears two twigs of what appears to be *Diosma aspalathoides* Lam. According to Aiton's *Hortus Kewensis* (1789) this species, under the name of *Diosma ericoides*, was in cultivation in 1756 by Mr Philip Miller who was in charge of the Chelsea Physick Garden at that time.

Both *Diosma rubra* L. and *Diosma ericoides* L. which apply in part to *Co-leonema album*, have been a long standing source of confusion. To this day *Co-leonema album* is marketed under the name of *Diosma ericoides* in New Zealand. Salisbury did not care for the name *Diosma rubra*, saying that it was inappropriate and substituted the name *Diosma juniperifolia* which he said was better.

SPECIMENS EXAMINED

CAPE—3318 (Cape Town): Saldanha Bay, Constable Hill, S.E. slope

(-AA), 26/4/1949, *Macnae 1075* (BOL); Langebaan Lagoon, 30/5/1972, *Axelson 566* (NBG); Table Mountain, Cape Peninsula (-CD), 10/11/1827, *Ecklon 239* (C, G, S), *Ecklon & Zeyher 831* (C, G, PRE, SAM), 1 000–2 000 ft., 28/7/1826, *Drège 7137* (PRE, K), 7138 (P), 7139 (G, P, S), -/6/1829, *Verreaux s.n.* (G), 2 000 ft., -/8/1883, *MacOwan H.N.A.A. 48* (BOL, BM, G, GRA), 30/11/1926, *Lynes s.n.* (BM), 23/9/1883, *Wilms 3019* (G), -/11/1919, *Rogers 17450* (G); amongst rocks above Postern Butress, 2 500 ft., -/8/1938, *Esterhuysen s.n.* (BOL 23265); Camps Bay, 11/8/1927, *Salter 245/9* (BM), 25/8/1917, *Stopford 57* (BM), -/12/1928, *Maude s.n.* (BM), 800 ft., -/11/1897, *Galpin 3852* (GRA, PRE); Stinkwater, 1875/1880, *Rehmann 1339* (BM), 18/8/1883, *Wilms 3108* (BM); above Kirstenbosch, 25/9/1952, *Salter 9482* (BM).

—3418 (Simonstown): rocky slopes of Little Lions Head, near Hout Bay, Cape Peninsula, (-AB), -/7/1939, *Esterhuysen s.n.* (BOL 23264, PRE); Llandudno, 18/9/1943, *Compton 14826* (NBG); Hout Bay, 17/8/1940, *Compton 9170* (NBG); Muizenberg Mt., -/7/1838, *Krauss s.n.* (G), 1 800 ft., -/12/1880, *H. Bolus 2741* (BM); Fish Hoek Valley, 18/8/1883, *Wilms 3108* (BM); Noordhoek, -/9/1929, *Dame Alice and the Misses Goodman 341* (BM), -/10/1929, *Dame Alice and the Misses Goodman 878* (BM); Kalk Bay Mt., 16/10/1946, *Barker 4205* (NBG); Kommetjie hills, 20/9/1949, *Barker 5897* (NBG); Schusters Bay, 30/10/1940, *Barker 1154* (NBG); Klaver Valley near Simonstown, 10/11/1933, *Barker s.n.* (BOL); in campos. et collibus prope Simonsbay frequens, -/10/1801, *R. Brown ? s.n.* (BM); Olifantsbosch, W. coast of Cape Peninsula (-AD), 7/10/1956, *Chamberlain 41* (BM); Steenbras Mouth, Somerset West Division (-BD), 6/9/1947, *Compton 13581* (NBG); Harold Porter Reserve, Caledon Division, 16/10/1963, *Martin 761* (NBG);

—3419 (Caledon): Sandbaai, Caledon Division (-AC), 29/9/1963, *Walters 209* (NBG); Hermanuspetersfontein, Caledon Division, 200 ft., -/7/1896, *F. Guthrie s.n.* (BOL), 50 ft., -/7/1896, *Bodkin s.n.* (BOL), 100 ft., -/9/1901, *H. Bolus 9855* (BOL); Voëlklip, Hermanus, near Mossel River Mouth, Caledon Division (-AD), 0–50 ft., 6/8/1971, *Williams 1500* (NBG), 10 m, 19/8/1975, *Williams 2047* (NBG), 11/11/1978, *Williams 2640* (NBG); Vogelgat Kloof, Caledon Division, 100 ft., 9/10/1978, *Williams 2602* (NBG); Gansbaai, Caledon Division (-CB), sea level, 13/10/1964, *Walters 279* (NBG); Franskraal Mtns., 14/4/1951, *Maguire 2639* (NBG); Brandfontein, amongst rocks along the coast, Bredasdorp Division (-DD), 15/10/1951, *Esterhuysen 19100* (BOL).

—3420 (Bredasdorp): amongst rocks at summit of ridge on S. side of Bredasdorp Mountain (-CA), 15/10/1951, *Esterhuysen 19150* (BOL); near Cape Infanta, rocky coast (-BD), 28/9/1959, *Esterhuysen 28323* (BOL).

Without precise locality: e. Cap. b. Spei. *Thunberg s.n.* (B-W 4729/1, C. LINN-Smith's Herb. 397.6, UPS-THUNB. 5657), C.B.S. *Lehmann s.n.* (BM), *Niven s.n.* (BM), *Roxburgh s.n.* (BM, G), *Stanger s.n.* (BM), *Harvey 452* (BM), *Bowie 47 and 50* (G), Swellendam, -/9/1827, *Verreaux s.n.* (G), -/10/1827, *Ver-*

reaux s.n. (G), *Diosma rubra* 3. as to L. hand specimen (LINN 270.4), as to L. hand specimen (LINN 270.5), (LINN 270.8), *Diosma rubra* (LINN-Smith's Herb. 397.5.1), *Diosma alba* (LINN-Smith's Herb. 397.6).

DISTRIBUTION AND BIOLOGY

Coleonema album appears to be very much a coastal plant, well able to withstand the strong winds which frequently blow in from the sea. The only population at any great distance from the sea lies at the southern end of the Bredasdorp Mountains about 19 km from the coast. Plants are found growing amongst outcrops of rocks of the Table Mountain Sandstone Series or of the underlying Cape Granite but never upon the coastal limestone of the Bredasdorp Series. The main population centre appears to be the Cape Peninsula. There is an outlier 95 km to the north at Saldanha Bay and a fairly even distribution along the coast from the Steenbras River Mouth to Gansbaai. From there eastwards there are isolated populations at Brandfontein, Bredasdorp and a final outlier 77 km still further to the east at Cape Infanta. Plants grow at sea level and at all altitudes up to a maximum of 750 m (2 500 ft.) on Table Mountain. The plants may form dense stands in coastal scrub. One plant 1.8 m tall showed about 25 growth rings. Flowering takes place mainly from August to October and ripe fruits may be found up to the end of November. The conspicuous white flowers and the nectariferous disc indicate that pollination is most probably effected by insects. The seeds when ripe are ejected by the usual catapult mechanism and regeneration takes place only from seed and usually only after fires. The leaves, when crushed, have a characteristic sweet smell but the scent of the flowers is not so pleasant. Most plants are parasitised by a gall insect which gives rise to a characteristic little conelike collection of leaflets often making herbarium material very easy to recognise.

No significant variation and no hybridisation have been observed.

DISCUSSION

In 1824 when Bartling and Wendland proposed the new genus *Coleonema*, *Diosma alba* Thunberg was the only species of *Coleonema* then known to science. The characters that distinguished it from species in other genera of the *Diosmeae* were stated by them as: (1) *calyx* 5-partite; (2) *hypogynous disc* not very free at the margin; (3) *petals* narrowed below, longitudinally grooved; (4) *filaments* 10, 5 fertile equalling the calyx, 5 sterile filiform, glabrous, connate within the groove of the petals; (5) *anthers* subrotund, gland adnate; (6) *style* short; (7) *stigma* capitate.

Coleonema album may be distinguished from all other species by having the (1) *staminode* mostly connate with the petal; (2) *flowers* white, 6–7 mm diam.; (3) *leaves* 12–13.5 mm long. The presence of a small conelike *gall*, found only in this species, is a useful character for identification.

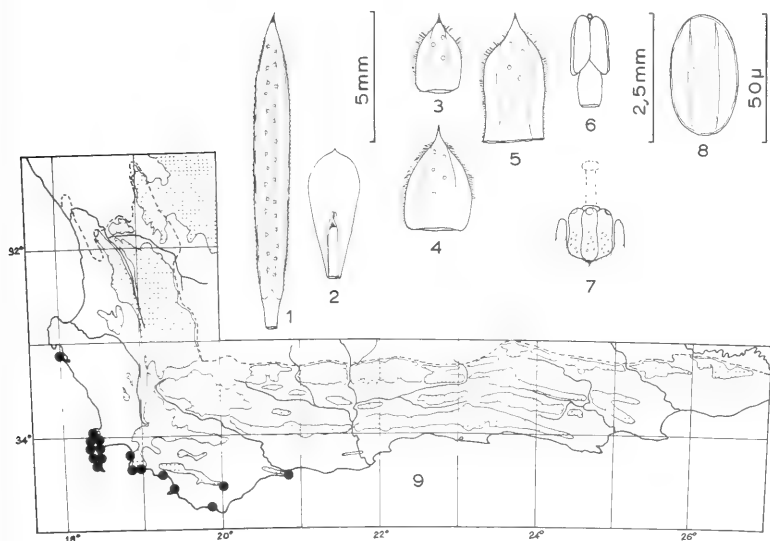


FIG. 8.

Coleonema album: 1, leaf. 2, petal with staminode. 3, uppermost bract. 4, bracteole. 5, calyx lobe. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

5. *Coleonema aspalathoides* A. Juss. ex Don, Gard. and Bot. 1: 783 (1831). Type: *Diosma aspalathoides* herb. Burm. non Lam. *Le Valliant?* s.n. (G. lectotype; P-JUSS 12 917 portion of lectotype).

(*Coleonema*) *D. aspalathoides* A. Juss. in Mém, Mus. Hist. Nat., Paris 13: 471 (1825), nom. nud.

Coleonema aspalathoides Juss. ex Sond. in Fl. Cap. 1: 378 (1860). Type: as above.

Coleonema dregeanum Presl., Bot. Bemerk: 31 (1844). nom. nud. Type: Zuurbergen, grassy heights near Strubels, 3 000 ft., 7/11/1829, *Drège* 2251 (BM, G, K, S).

Shrubs forming dense stands, 0.5–1.3 m tall, dense, bushy, branching from near the base. *Branches* numerous, fairly erect, not very straight, glabrous, smooth, reddish-brown. *Branchlets* very numerous, very slender, erect, minutely puberulous, not hidden by the leaves. *Inflorescence* solitary, terminal on very short branchlets that may be so reduced and numerous that the flowers appear to be axillary and/or crowded into spikes; flowers 8–10 mm diam., petals pink, throat open, subtended by several reduced leaves. *Leaves* up to 12 mm long, perhaps slightly longer in young plants, 1–1.2 mm broad, linear-oblong, acute

glabrous, dark green, alternate, spreading-erect; apex often reflexed with a sharp point about 1 mm long; narrowed at the base to a reddish petiole about 1 mm long; margins narrowly translucent, minutely serrulate; abaxial surface rounded, irregularly gland-dotted in two rows towards the midrib. *Bract* 1,6–1,8 mm long, 0,8–1 mm broad, ovate, acute, recurved-apiculate, partly puberulous; margins ciliate, broadly translucent; gland-dotted towards the midrib. *Bracteoles* two, 1,7 mm long, 1 mm broad, ovate, acute, apex elevated, margins ciliate, broadly translucent, pubescent above to either side of the midrib. *Calyx lobes* five, 2,5 mm long, 1,3 mm broad, sub-ovate, apex tapering with a long sharp reddened recurved point; margins broadly translucent, villous-ciliate; abaxial surface puberulous to either side of the midrib; adaxial surface minutely pubescent at the middle. *Petals* five, 5,5 mm long, 2,2 mm broad, obovate, apiculate, narrowing evenly to the base; limb pink, spreading; *claw* sparsely ciliate, sparsely pubescent below and at the apex of the staminode. *Staminodes* five, 2 mm long, 0,4 mm broad, linear, white, obtuse with a minute yellowish apical gland 0,1 mm long, connate with the claw of the petal below but not enfolded. *Filaments* five, becoming 2,3 mm long after anthesis, glabrous, subulate. *Anthers* five, 1 mm long, 0,7 mm broad, orange-yellow with a minute pointed apical gland. *Pollen* 42 μ long, 25–30 μ broad, spherical to sub-cylindric. *Disc* obvallate, thin, dark green, exceeding the ovary. *Stigma* 0,65 mm diam., depressed globose, capitate. *Style* becoming 1 mm long, erect, glabrous, rather slender. *Ovary* 5-carpellate, 0,8 mm long, 0,7 mm diam., glabrous, apices globose. *Fruit* 5-carpellate, 4,5 mm long, 3,5 mm diam., carpels glabrous with a prominent midrib and lateral ribs; *horns* 1 mm long, erect, apex somewhat hoof-shaped. *Seed* 2,5 mm long, 1,2 mm broad, black, shining; aril brownish.

The description given by Don (1831) of *Coleonema aspalathoides* agrees very well with the type which he cited (*Diosma aspalathoides* herb. Burm. but not of Lam.) with the one exception that he gives the colour of the flowers as white whereas in fact the flowers are always pink. This discrepancy can be explained as follows: the type specimen in the Burman herbarium (now at Geneva) was at the time in the Delessert herbarium in Paris. It was examined by Adrien de Jussieu who detached a small fragment which he placed in his own herbarium (P-JUSS 12 917). Don studied de Jussieu's work on the Rutaceae (1825) and must have examined one or other of the specimens of *D. aspalathoides*. As this species was never in cultivation, Don could only base his description upon the dried type material, then nearly 50 years old when he saw it, and, knowing only *Coleonema album* with white flowers, must have presumed that his plant also would have white flowers.

With regard to the specimen in Burman's herbarium at Geneva, we can presume that this material came into his possession after 1786 (the date of publication of Lamarck's *Encycl. Meth. Bot.* which he cites) and before his death in



FIG. 9.

Coleonema aspalathoides: lectotype in Burman's herbarium at Geneva.

1793. It is possible that the words "Cap. Le V." (Fig. 9) written on the label by Burman refer to collection by *Le Valliant* who returned to Holland from the *Cape* in 1784. Some person has attributed the specimen to *M. Lemmonier*, apparently reading *Cap. Le V.* as *Cap. Le M.*, Louis Guillaume Le Monnier Professor at the Jardin des Plantes from 1758 to 1785 but who could never have collected at the Cape. This specimen in Burman's herbarium at Geneva, a single branch about 350 mm long, having been cited by both Don and de Jussieu, is therefore chosen as the lectotype.

SPECIMENS EXAMINED

CAPE—3323 (Willowmore): Foothills of Kouga Mtns. at Braam River near Joubertina, Uniondale Division (-DB), 28/10/1949, *Esterhuysen 16330* (BOL, NBG); Joubertina, Uniondale Division (-DD), -/7/1942, *C. J. Esterhuysen s.n.* (BOL, NBG).

—3324 (Steytlerville): Kouga Mtns. near Kouga Peak, lower E. slopes, Uniondale Division (-CA), 14/11/1944, *Esterhuysen 10802* (BOL, GRA, NBG); Kouga River, on road to Nooitgedacht, Humansdorp Division (-CC), 1 000 ft., 26/8/1975, *Williams 2060* (NBG, S); Kromme River (-CD), *Niven? 21* (BM, S); Assegaibosch, Humansdorp Division, 900–1 000 ft., 1/8/1912, *Rogers 2853* (BOL, GRA, SAM); Zuuranys Pass above Karreedouw, Humansdorp Division, 1 200 ft., 8/9/1973, *Thompson 1817* (K); Kromme River, N. of Assegaibosch, Humansdorp Division, 900 ft., -/5/1923, *Fourcade 2605* (K); Kromme River, W. of Humansdorp, 400 ft., 11/9/1960, *Acocks 21477* (K, NBG); Tuschen Bij, Humansdorp Division, 1 200 ft., -/9/1909, *Fourcade 5649* (BOL, GRA).

—3325 (Port Elizabeth): Bassonskloof, Annies Villa, Somerset East Division (-BD), 3 000 ft., 11/8/1965, *Bayliss 2950* (NBG); Suurberg Pass, Somerset East Division, 3 000 ft., 13/8/1973, *Bayliss 5895* (NBG); Zuurbergen, grassy heights near Strubels, 3 000 ft., 7/11/1829, *Drège 2251* (BM, G, K, S).

—3420 (Bredasdorp): 125.10, In collibus ad Rietkuil, Swellendam (-BA), -/10/-, *Zeyher 2159* (C, G, GRA, K, P, PRE, S, SAM, TCD); On farm Uitvlugt, Heidelberg Division, 14/9/1962, *van Breda 1582* (K, PRE); N. of Verkykerskop, Heidelberg Division, 750 ft., 21/1/1975, *Williams 1954* (NBG); Verkykerskop, S. side on Soutkloof, Heidelberg Division, 750 ft., *Williams 2023* (NBG, S); Heidelberg Division, -/7/1939, *Leipoldt 3358* (BOL, GRA, NBG, PRE); Potberg, W. Base, Bredasdorp Division (-BC), 13/10/1940, *Pillans 9347* (BOL, G, NBG, PRE).

—3421 (Riversdale): Hills near Riversdale (-AB), 400–600 ft., -/7/1923, *Muir 2970* (GRA, PRE); Plaatjieskop, Riversdale Division, 240 m, 3/5/1974, *Williams 1897* (NBG, PRE, S).

Without precise locality: *Roxburgh s.n.* (BM), *Bowie 101* (BM), *Thunberg s.n.* (S), *Le Valliant? s.n.* (P-JUSS 12 917, G).

DISTRIBUTION AND BIOLOGY

Coleonema aspalathoides is found at altitudes varying from 120 to 900 m above sea level. The distribution is split into three areas with very large disjunctions, the total distance from east to west being about 500 kilometres. At the western end, towards Swellendam, relic populations are found on a few isolated silcrete-capped hills surrounded by soils derived from the Bokkeveld shales; the central populations appear to be associated with the Table Mountain Sandstone and in the east on the Suurberg Pass one finds the plants growing on soils de-

rived from the Witteberg series. In spite of these differences in altitude, distance and soils no appreciable variation has been noted in the species.

The wide-open flower with its dark green disc and sticky pollen leads one to assume that it is most probably pollinated by insects. The plants are destroyed by fires and regeneration can only take place from seed which is ejected by the usual catapult mechanism when ripe. Flowering has been observed at different localities from April until November and ripe fruits in October and November. The leaves are not strongly or sweetly scented but the fruits when crushed have the strong smell of amylacetate.

DISCUSSION

The following characters when considered together definitely place this plant in the genus *Coleonema* and exclude it from any other genus of the *Diosmeae*: (1) flowers solitary with several bract-like basal leaves, terminal or axillary; (2) petals connate with the staminode below; (3) anther with a minute apical gland; (4) disc obovate; (5) stigma capitate; (6) style and filaments short, glabrous, erect; (7) ovary 5-carpellate.

Coleonema aspalathoides is a distinct species with leaves that have a dark green colour, somewhat reflexed above with a long sharp point, with petals having a short broad claw that is pubescent and ciliate below, a blade relatively narrow so that they do not overlap each other at the margins. It is nearest in appearance to *Coleonema pulchellum* Williams which however has the bracts, bracteoles and sepals always glabrous on the outside. The differences in the flowers are as shown below:

C. aspalathoides
flowers 8–10 mm diam.
petals obovate with a longer apiculus;
with spaces between;
edges somewhat incurled;
gradually recurved at throat;
sparsely gland-dotted;
surface irregular with large watery cells;
staminodes deeper in throat.

C. pulchellum
flowers 7 mm diam.
petals orbicular with a minute apiculus;
more nearly touching;
edged fairly flat;
abruptly recurved at throat;
without any gland dots;
surface smooth;
staminodes protrude.

ACKNOWLEDGEMENT

I wish to acknowledge with deep gratitude the assistance received from Dr. Heino Heine of the Muséum National D'Histoire Naturelle in Paris in examining closely the specimen of *C. aspalathoides* in the Jussieu Herbarium and for his comments on this matter.



FIG. 10.
Coleonema aspalathoides: flower, 8 mm diam.

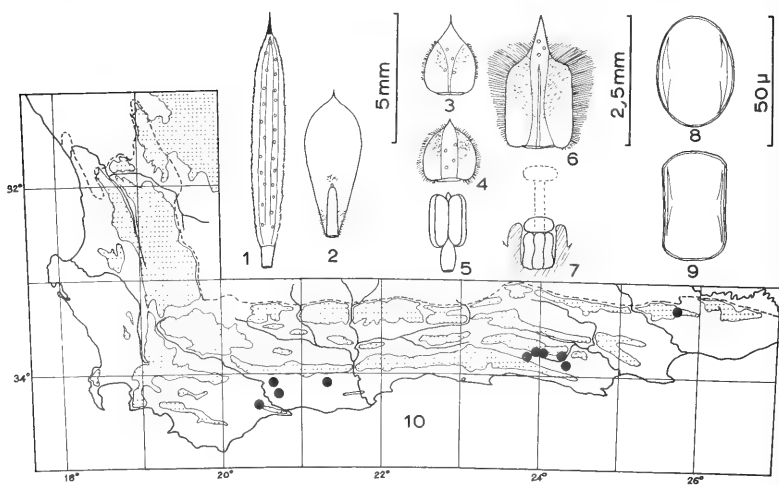


FIG. 11.
Coleonema aspalathoides: 1, leaf. 2, petal with staminode. 3, uppermost bract. 4, bracteole. 5, anther. 6, calyx lobe. 7, gynoecium and disc. 8 and 9, pollen. 10, distribution.

6. *Coleonema pulchellum* Williams, sp. nov. affinis *C. aspalathoides* Juss. ex Don sed bractis, bracteolis sepalis et petalis extus glabris, petalis anguste unguiculatis, sepalis non villosociliatis, stylo crassiore differt.

Frutex 800 mm, densus, erectus, ad basin monocaulis. *Rami* erecti, graciles, numerosi. *Ramuli* erecti, graciliores, numerosi, minute puberuli, foliosi. *Folia* 8–10 mm longa, 0.8 mm lata, lineari-lanceolata, pungentia, petiolata, bifariam glanduloso-punctata, glabra erecta, alterna, marginibus anguste hyalinis denticulato-serrulatis. *Inflorescentia* solitaria, terminalis vel axillaris; *flos* 7–8 mm diam., roseus. *Bractea* intima 2 mm longa, 1.2 mm lata, deltoidea, pungentia, glabra, costa virida glanduloso-punctata, marginibus late hyalinis, ciliatis. *Bracteolae* duae, 2 mm longae, 1.3 mm latae, deltoideae, pungentiae, extus glabrae, intus pubescentiae, costa virida glanduloso-punctata, marginibus late hyalinis, ciliatis. *Sepala* quinque, 2 mm longa, 1.3–1.4 mm lata, late oblonga, apiculata, intus pubescentia, extus glabra, costa virida glanduloso-punctata, marginibus late hyalinis crispo-ciliatis. *Petala* quinque, 5–5.7 mm longa, 2.3–2.8 mm lata, glabra, roseus; *limbus* orbicularis, apiculatus, patens, marginibus indistincte hyalinis; *unguis* 2.2 mm longus, 1 mm latus, ad basin staminodio connatum. *Staminodia* quinque, 2.2 mm longa, 0.5 mm lata, glandula coronata, partim petalis connata. *Fila* quinque, 2 mm longa, glabra. *Antherae* quinque, ante anthesin 1.1 mm longae, 0.7 mm latae, flavidae, glandula coronata. *Pollen* 45 μ longum, 22 μ latum, oblongum. *Discus* viridus, succulentus, obvallatus, ovarium aequans. *Stigma* 0.5 mm diam., globosum, capitatum. *Stylus* 1.1 mm longus, erectus, glaber, persistens. *Ovarium* 5-carpellatum, 0.9 mm longum, 0.8 mm diam., glabrum. *Fructus* 5-carpellatus, 5.1 mm longus, 4.5 mm diam., glaber, marginibus multi-glanduloso-punctata; *cornua* 1.2 mm longa, erecta, emarginata, extus immerso-apici-glandulata. *Semen* 2.8–2.9 mm longum, 1.5 mm latum, piceum, nitens.

Type: CAPE—3325 (Port Elizabeth): Winterstrand, Port Elizabeth, flat ground behind the coastal dune (-DC), sea level, 26/8/1975, Williams 2056 (NBG, holotype; BOL, K, L, MO, NSW, PRE, S, STE, isotypes).

Shrubs 800 mm tall, dense, erect, single-stemmed at base. *Branches* numerous, erect, slender; bark brownish; cuticle splitting. *Branchlets* very numerous, erect, slender, leafy, densely and minutely puberulous. *Leaves* 8–10 mm long including petiole 1 mm long, 0.8 mm broad, linear-lanceolate, acute, pungent, alternate, erect; hyaline margins narrow, denticulate-serrulate with teeth pointing upwards; adaxial surface glabrous except at the petiole, flat when fresh; round-backed, glabrous with one row of gland dots to either side of the midrib. *Inflorescence* solitary, terminal on short branchlets or axillary on very much reduced branchlets often crowded towards the tops of the branches; flowers 7–8 mm diam., pink to almost white in colour. *Bract* the uppermost four leaves by degrees alter into bracts, the last below the two bracteoles being 2 mm long, 1.2 mm broad, deltoid, glabrous; midrib green, gland-dotted, produced into a pun-

gent apex with 2 hairs at the tip; margins ciliate, broadly translucent. *Bracteoles* two, 2 mm long, 1,3 mm broad, deltoid, pubescent inside above otherwise glabrous; midrib green, gland-dotted, produced into a pungent apex with or without a single hair at the tip; margins ciliate, broadly translucent. *Calyx lobes* five, 2 mm long, 1,3–1,4 mm broad, broadly oblong, pubescent adaxially otherwise glabrous; midrib green, gland-dotted, apiculate; margins crisped ciliate, broadly translucent. *Petals* five, 5–5,7 mm long, glabrous; *limb* 2,3–2,8 mm broad, orbicular, apiculate, pink, spreading; *claw* 2,2 mm long, 1 mm broad above, 0,5 mm at base; midrib connate with the staminode but grooved and free above. *Staminodes* five, 2,2 mm long, 0,5 mm broad, narrowing to a small glandular apex, connate with the petal except right at the tip, equalling the claws and the spent anthers. *Filaments* five, 2 mm long, glabrous, erect, acicular. *Anthers* five, before anthesis 1,1 mm long, 0,7 mm broad, yellow, with a minute sessile, globose apical gland. *Pollen* 45 μ long, 22 μ broad, oblong. *Disc* slightly wavy, erect, equalling the ovary, dark green, fleshy with petals staminodes and anthers arising at the base. *Stigma* 0,5 mm diam. globose, capitate. *Style* becoming 1,1 mm long, erect, glabrous, persisting. *Ovary* 5-carpellate, 0,9 mm long, 0,8 mm diam., glabrous; carpels with globose apices. *Fruit* 5-carpellate, 5,1 mm long, 4,5 mm diam., glabrous; carpels dimpled and laterally ridged with many gland dots; *horns* 1,2 mm long, erect, emarginate; apical gland immersed facing outwards. *Seed* 2,8–2,9 mm long, 1,5 mm broad, black, shining.

The "Confetti Bush" has long been cultivated in gardens where it has been known by the name *Coleonema pulchrum*. Ecklon and Zeyher (1835) were the first to list their collections of this plant from the Eastern Cape under this name. In *Flora Capensis*, Sonder (1859/1860) included plants from both the Swellendam District and from the Eastern Cape near Port Elizabeth under *C. pulchrum* Hook. His synonymy includes no less than four distinct taxa. The specimen from which Hooker prepared his drawing and description of *Coleonema pulchrum* in *Curtis's Botanical Magazine* (1834) is preserved in the herbarium at Kew and this plant with its leaves 35 mm long and 15 mm diam. is very plainly different from *Coleonema pulchellum* here described with leaves 10 mm long and flowers 0,8 mm diam. Hooker's specimen was cultivated in the Botanical Garden at Glasgow and similar plants have been found in the wild in the vicinity of Swellendam from whence the seed must have been originally obtained.

The first person actually to collect specimens of *C. pulchellum* was Burchell who found it in December 1813 at Algoa Bay. It seems regrettable that he made so little use of his collections which were unique and far better recorded than any before his time.

SPECIMENS EXAMINED

CAPE—3423 (Knysna): Robberg near Plettenberg Bay, Knysna Division (-AB), 500 ft. alt., 4/5/1952, Taylor 380 (NBG); cliffs on S.E. side, 25/10/1955,

Esterhuysen 25010 (BOL); Witsand, 350 ft., 25/8/1975, *Williams 2051* (NBG).

—3424 (Humansdorp): Klipdrift, Humansdorp Division (-BA), May/June 1930, *Thode A2468* (K, PH, PRE).

—3325 (Port Elizabeth): at the upper part of the Lead Mine River (-CD), 7/2/1814, *Burchell 4616* (K); flats between Krakakamma and Vanstaadensberg, 500–1 000 ft., -7/-, *Zeyher 5.7* (BOL, C, E, G, GRA, PRE); between Vanstaadensberg and Bethelsdorp, under 1 000 ft., IV C.c.15, -12/-, *Drège 7143* (G, K, P); in collibus prope Bethelsdorp et in planitie magna sub montes Vanstaadensberge altit. II (Uitenhage), -7/-, *Ecklon & Zeyher 836* (C, G, K, PRE); Cape Road 12th mile, Port Elizabeth, 7/8/1932, *Long 692* (GRA, K, PRE); west of Port Elizabeth towards Witteklip, 26/8/1947, *Rodin 1020* (BOL, K, PRE); at Algoa Bay near the Burying Ground (-DC), 11/12/1813, *Burchell 4316* (K); at Algoa Bay near the Block House, 13/12/1813, *Burchell 4346* (K); in a walk by the Baakens River under Fort Frederick, 14/12/1813, *Burchell 4352* (K); Uitenhage, on the downs along the strand of Algoa Bay, by Port Elizabeth and Cape Recife, -12/-, *Zeyher 747* (BM, K, NGB, PRE); in moist places Walmer Flats near Port Elizabeth, 300 ft. alt., -9/1868, *H. Bolus 1901* (BOL); Port Elizabeth, Birchells Valley, 27/7/1895, *H. Bolus s.n.* (NBG, *Guthrie 3762*); beach, Port Elizabeth, -1/1907, *Potts 306* (BOL, GRA, PRE); Humewood near Port Elizabeth, -8/1912, *Paterson 780* (BOL, GRA), -9/1921, *Cruden 323* (PRE), 6/7/1947, *Urton 23* (GRA), *Urton 57* (GRA), 26/4/1962, *Dahlstrand 92* (C), -9/1911, *Daly 1068* (GRA), -8/1906, *West 48* (GRA, K), 4/8/1931, *Long 433* (K, PRE), -6/1900, *Sim 41* (PRE), -10/1900, *Sim B14* (PRE), -11/1900, *Sim s.n.* (PRE), -9/1960, *Haasbroek 1876* (PRE), 6/8/1944, *Long 1482* (PRE), 1483 (PRE), 26/2/1961, *Dahlstrand 14* (PRE); Winterstrand at sea level, 26/8/1975, *Williams 2056* (NBG, BOL, K, L, MO, NSW, PRE, S, STE).

—3425 (Skoenmakerskop): within 2 miles of Skoenmakerskop, Port Elizabeth (-BA), -10/1921, *Forest Department Port Elizabeth 29* (GRA); Skoenmakerskop, Port Elizabeth, sea shore, 20 ft. alt., 5/7/1925, *Borle 1* (K, PRE).

—3326 (Grahamstown): Alexandra Division, Bushmans River Mouth, along banks of the spring Klipfontein (-DA), 200 ft. alt., 28/8/1952, *Archibald 4542* (PRE).

DISTRIBUTION AND BIOLOGY

Coleonema pulchellum is found mainly in the Port Elizabeth area along the coast towards Cape Recife and on the plains around Greenbushes with outliers on Robberg at Plettenberg Bay 180 km to the west, and at the Bushmans River Mouth 100 km to the east. It occurs at altitudes from sea level near Port Elizabeth up to 150 m (500 ft.) on Robberg, growing in windblown sandy soil with deposits of coastal limestone not far away. The flowering season appears to be from March to October and fruits have been found from August to January. The presence of conspicuous spreading petals and a fleshy disc in the flower with the

style lengthening only after anthesis would indicate that this plant is most probably pollinated by insects. Seed when ripe is scattered by the usual catapult mechanism. The leaves have a pleasant sweet smell when crushed.



FIG. 12.

Coleonema pulchellum: flower, 7–8 mm diam.

DISCUSSION

Having the staminode connate with the petal, looking very much as though it lies within a groove in the petal, places this species in the genus *Coleonema*. Other characters that exclude this plant from other genera of the *Diosmeae* are: (1) *flowers* solitary, terminal or axillary on reduced branchlets; (2) *petals* clawed, spreading; (3) *anther* with a minute apical gland; (4) *disc* obvallate; (5) *stigma* 0,6 mm diam., capitate; (6) *style* and *filaments* short, glabrous, erect; (7) *ovary* 5-carpellate.

Coleonema pulchellum is a distinct species resembling *C. aspalathoides* Juss. ex Don but differing in having bracts, bracteoles, sepals and petals always glabrous on the outside, petals with narrow claws, sepals not villous-ciliate and the style somewhat thicker. It differs from *C. pulchrum* Hook. and *C. virgatum* E. & Z. from the Langeberg near Swellendam, which have much longer leaves and larger flowers. All other species of *Coleonema* have very small white flowers.

7. *Coleonema virgatum* (Schidl.) Ecklon & Zeyher, Enum. Plant.: 106 (1835).
Coleonema album (Thunb.) Bartl. & Wendl. var *B. virgatum* Schidl. in *Linnaea*

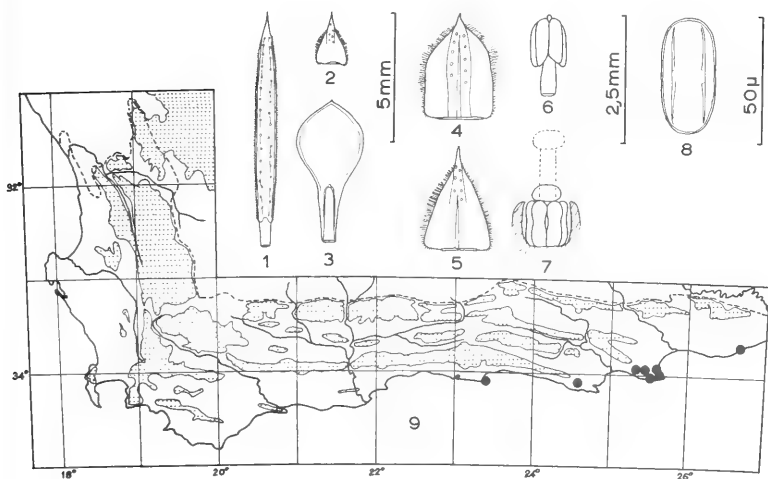


FIG. 13.

Coleonema pulchellum: 1, leaf. 2, uppermost bract. 3, petal with staminode. 4, calyx lobe. 5, bracteole. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

6: 199 (1831). Type: Duivelsbosch bei Swellendam, 16/10/1826 (or 1828) *Ecklon s.n.* (SAM, lectotype; S, isotype).

Shrubs probably up to 1 m tall, arising from a single stem at base. *Branches* fairly straight, glabrous, dark brown, smooth with transverse leaf scars becoming double-lipped when old. *Branchlets* fairly numerous, slender, straight, erect, glabrous, tinged with red. *Leaves* 26–32 mm long including petiole about 1.5 mm long, 1.2–1.3 mm broad, linear, acute-subulate, glabrous, spreading-erect, alternate; margins narrowly translucent, minutely serrulate with erect sharp points; adaxial surface flat; abaxial surface rounded, multi-gland-dotted to either side of the midrib. *Inflorescence* solitary, terminal or axillary, sessile, pale pink or white. *Bract* 4.5 mm long, 0.9 mm broad, linear-lanceolate, subulate; margins ciliate, broadly translucent below, rolled in above; adaxially very sparsely pubescent along the midrib; abaxially glabrous, gland-dotted, midrib prominent below. *Bracteoles* two, 3.3–3.4 mm long, 1.1 mm broad, lanceolate, subulate; margins ciliate, broadly translucent below, rolled in above; adaxially sparsely pubescent along the midrib; abaxially glabrous, gland-dotted above. *Calyx lobes* five, 3.5 mm long, 1.4 mm broad, oblong, subulate above with a long sharp point; margins ciliate, broadly translucent below, rolled in above; adaxially sparsely pubescent towards the midrib; abaxially glabrous, gland-dotted above.

Petals five, 6,3–6,5 mm long overall, 2,7–3 mm broad, elliptic, apiculate, glabrous, eglandular, without any translucent margins; *claw* 2,7 mm long, connate with the staminode with an elevated groove running 0,6 mm up above the apex of the staminode. *Staminodes* five, 2,3 mm long, connate with the claw of the petal except at the apex which is tipped with a small gland. *Filaments* five, becoming 2 mm long, erect, glabrous. *Anthers* five, 0,6 mm long, 0,5 mm broad, yellow; apical gland small, somewhat pointed. *Pollen* 30 μ long, 21 μ broad, ellipsoid. *Disc* obvallate, exceeds the ovary, equals the top of the stigma at first, fairly narrow and level on top. *Stigma* 0,5 mm diam., depressed globose, sessile at first. *Style* erect, glabrous, becoming 1 mm long, persisting. *Ovary* 5-carpellate, 0,8 mm long, 0,8 mm diam., glabrous; apices globose with an immersed gland. *Fruit* 5–5,5 mm long, 4,5 mm diam., glabrous, gland-dotted; horns 1 mm long, incurved-erect, with an immersed gland facing outwards at the tip. *Seed* 3,3 mm long, 1,5 mm broad, black, shining.

Coleonema virgatum was collected by Ecklon on the 16th October (1826 or 1828) on the mountain slopes above Duivelsbos at Swellendam. Duivelsbos is an indigenous forest to the north of Swellendam on the south slopes of the Langeberg. Sheets so labelled are to be found at SAM and S. What appears to have been a separate collection of the same species possibly made by Zeyher from above Puspasvalley is labelled *Coleonema virgatum* E.Z. 70.10. Sheets so labelled are to be found at C, E and S. Specimens possibly distributed by both Ecklon and Zeyher bearing their usual printed label extracted from their *Enumeratio* (1835) giving both the above localities and numbered 832 are to be found at C, E, S and SAM.

Von Schlechtendal's herbarium is reputed to be at Halle in East Germany but inquiries there have failed to establish this; nor is there any material still extant at Berlin. For this reason and until the specimen actually seen by von Schlechtendal is found, a specimen in the collection of the South African Museum Herbarium at Kirstenbosch has been chosen as the lectotype. The validity of other specimens at C, E, S and SAM remains doubtful. The relevant sheet in the herbarium of the South African Museum bears two specimens. On the right hand side is a twig of *C. virgatum* about 430 mm long, without flowers or fruits, with Ecklon and Zeyher's usual printed label. On the left hand side is a twig, which has been chosen as the lectotype, about 280 mm long bearing both flowers and fruits and with a label bearing the inscription *Duivelsbosch bei Swellendam, Oct. 16* in Ecklon's hand. This is the locality mentioned by von Schlechtendal when he described *C. album* var. *virgatum* in *Linnaea* (1831).

Puspasvalley, which is not marked on modern maps, is more or less the area known as the Hermitage. It was above this farm that the Rev. T. M. Wurts made two collections of *C. virgatum* in 1952 on the south ridge of One O'clock Peak. As far as is known no other collections have ever been made in this vicinity.

SPECIMENS EXAMINED

CAPE—3320 (Montagu): Duivelsbosch bei Swellendam (-CD), 16/10/1826 (or 1828), *Ecklon s.n.* (S, SAM); *Coleonema virgatum* E.Z., 70.10, *Zeyher ? s.n.* (C, E, S); In lateribus montium prope Swellendam supra Duivelsbosch er Puspasvalley, Altit. IV, Oct., *Ecklon & Zeyher* 832 (C, E, S, SAM); One O'clock Mountain, south ridge, Swellendam, 3 000–4 000 ft., 30/6/1932, *Wurts* 204 (NBG), 16/8/1952, *Wurts* 204a (NBG). *not Ny Alversda.*
 —3321 (Ladismith): Garcias Pass, mountain slopes, Riversdale Division, (-CC), -/9/1908, *Phillips* 347 (SAM); Garcias Pass, wooded valley opposite Toll House, Riversdale Division, 1 200 ft., -/9/1897, *Galpin* 3856 (GRA).

DISTRIBUTION

Very few collections of this plant have been made. Its occurrence in the mountains above Swellendam to the west and above Riversdale to the east is rather odd because in between above Heidelberg one finds a very closely related species *C. pulchrum* Hook. If and when more material becomes available it may be possible to reassess the status of *C. virgatum*.

DISCUSSION

Having the staminode connate with the petal places this plant within the genus *Coleonema*. Other characters which exclude this plant from other genera of the *Diosmeae* are: (1) *flowers* solitary, terminal or axillary; (2) *petals* glabrous, clawed, spreading; (3) *anther* with a minute apical gland; (4) *disc* obvalate; (5) *stigma* 0.5 mm diam., capitate; (6) *style* and *filaments* short, glabrous, erect; (7) *ovary* 5-carpellate.

Coleonema virgatum is a distinct species with pale pink or white flowers resembling *C. pulchrum* Hook. but differing in having somewhat longer leaves, with bracts, bracteoles and calyx lobes subulate towards the apex and with smaller flowers with petals without any gland dots. It differs from both *C. aspalathoides* and *C. pulchellum* which have shorter leaves. All other species of *Coleonema* have white flowers.

8. *Coleonema pulchrum* Hook. in Curtis's Bot. Mag. 61: 3340 (1834). Type: *Hort. Glasgow s.n.* (K, lectotype). Matches plate 3340 in Curtis's Bot. Mag.

Diosma angustifolia Hort. Curtis's Bot. Mag. 61: 3340 (1834), nom. nud.

Shrubs to 1.2 m tall, erect, virgate, arising from a single stem at base. *Branches* erect, slender; bark splitting becoming light brown, smooth with small rather distant leaf scars. *Branchlets* erect, slender, minutely puberulous, hidden by the leaves. *Leaves* to 35 mm long on vigorous young stems, more usually 15–18 mm long including petiole about 1 mm long, 1–1.2 mm broad, linear, acute, mucronate, glabrous, pale green, straight, erect, loosely imbricate, alternate; margins minutely ciliolate becoming smooth; adaxially concave; abaxially

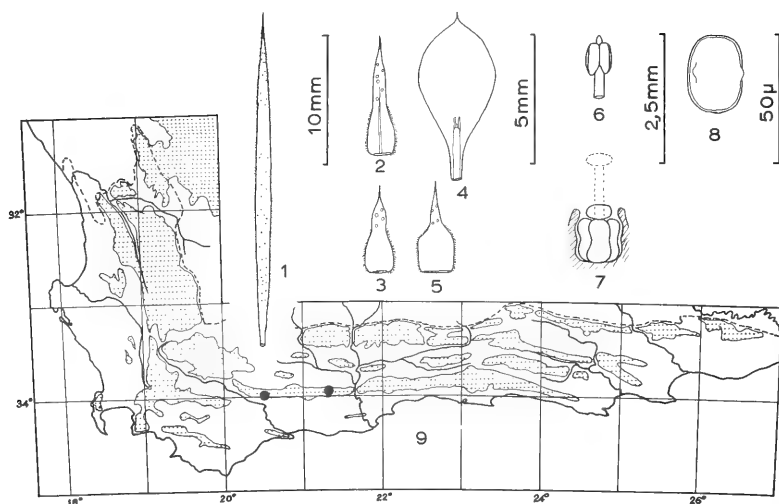


FIG. 14.

Coleonema virgatum: 1, leaf. 2, uppermost bract. 3, bracteole. 4, petal with staminode. 5, calyx lobe. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

convex, gland dots scattered \pm in two rows to either side of the midrib. *Inflorescence* solitary, terminal or axillary in the uppermost leaves, 12–13 mm diam., pink. *Bracts* five, increasing evenly in size from 1,4 mm long, 0,4 mm broad at the base to 3,6 mm long, 1 mm broad below the bracteoles, oblong to lanceolate, acute with a small sharp mucro; margins ciliolate, narrowly translucent; adaxially very sparsely pubescent; abaxially glabrous, gland-dotted to either side of the midrib. *Bracteoles* two, 3,4 mm long, 1,2 mm broad, lanceolate, acute, apiculate, ciliolate with broad translucent margins, glabrous, gland-dotted and reddened along the midrib; adaxially pubescent. *Calyx lobes* five, 3 mm long, 1,5 mm broad, broadly lanceolate, acute, apiculate; margins broadly translucent, ciliolate; adaxially pubescent; abaxial surface glabrous, gland-dotted and reddened along the midrib. *Petals* five, 7,6–8,5 mm long overall; limb 5,3 mm long, 3,6–4,2 mm broad, obovate, apiculate, glabrous, gland-dotted on the underside, pink, spreading; *claw* 2,5 mm long, narrowing to 0,4 mm wide at the base, glabrous, connate with the staminode except above where, two small pointed processes surround the apical gland of the staminode on either side. *Staminodes* five, 2,5 mm long, 0,3 mm broad, connate with the petal except above; apical gland conical, exudes nectar. *Filaments* five, becoming 1,7 mm long, acicular, glabrous, erect. *Anthers* five, 1,1 mm long, 0,6 mm broad, yellow; apical gland small, globose, exudes nectar. *Pollen* 47 μ long, 27 μ broad,

ellipsoid. *Disc* obvallate, margin free, exceeds the ovary, equalling the stigma, fairly narrow, level above, green, exudes nectar. *Stigma* 0.4 mm diam., capitate, depressed globose. *Style* becoming 1.3 mm long, slender, glabrous, erect, persisting. *Ovary* 5-carpellate, 0.8 mm long, 0.8 mm diam., glabrous, apices globose. *Fruit* 5-carpellate, 5.5 mm long (6.7 mm long to the tips of the horns), 4.7 mm diam., 6.7 mm broad across the horns, green, glabrous, many gland-dotted; *horns* 2 mm long, spreading and curved up slightly; apices emarginate clasping an immersed gland. *Seed* 4.6 mm long, 1.8 mm broad, black, shining; aril black capped.

W. J. Hooker in describing this plant in *Curtis's Botanical Magazine* stated that it had "long been cultivated in the greenhouse of the Botanic Garden of Glasgow under the name of *Diosma angustifolia*". A specimen preserved in the herbarium at Kew, annotated "Hort. G. L. (Glasgow)" is apparently the flowering twig from which Hooker prepared his excellent drawing in 1834. It has been chosen as the lectotype.

SPECIMENS EXAMINED

CAPE—3320 (Montagu): Tradouw Pass near the cave, Heidelberg Division (-DC), 1 000 ft., 2/11/1975, *Williams 2131* (NBG); Tradouw Pass, south side, amongst rocks, 4/9/1955, *Esterhuysen 24612* (BOL, PRE), 9/9/1924, *Compton 3447* (BOL), 3 000 ft., -/9/1917, *Marloth 7757* (PRE), -/10/1917, *Marloth 8621* (PRE), 29/9/1947, *Walgate 915* (PRE), 1 000 ft., 24/9/1949, *Acocks 15449* (PRE, K), 24/9/1949, *Sidey 1794* (PRE, S), 6/8/1950, *Martin 401* (NBG), 6/8/1950, *Bar-ker 7377* (NBG); Tradouw Pass, kloof beyond highest point, w. facing amongst rocks, 390 m, 4/12/1978, *Williams 2654* (NBG); Tradouw Peak and ridge above Pass, 2 500–4 400 ft., 5/9/1977, *Esterhuysen 34618* (BOL); Zuurbraak Mountain, wooded gorge, 1 000 ft., -/10/1897, *Galpin 3855* (GRA, PRE); Zuurbraak Peak, Swellendam, -/10/1925, *Barnard s.n.* (SAM).

Without precise locality: *Diosma conspicua*, Prom. B. Spei. -/1771, *Banks & Solander s.n.* (BM), *Verreaux s.n.* (G.)

Cultivated specimens: *Hort. Glasgow* (K), Bot. Gard. Edinburgh, 3/5/1841, *Graham s.n.* (G), -/4/1845, *Mus. de Hist. Nat. de Paris* (G), -/1850, *Hort. Kew* (S), -/1853, *Hort. Schonbrunn* (S).

DISTRIBUTION AND BIOLOGY

The distribution of *Coleonema pulchrum* appears to be extremely limited. It has only been found in the vicinity of the Tradouw Pass extending perhaps five kilometres to either side on the southern slopes of the Langeberg. It grows in rocky places at altitudes from 305 to 1 340 metres. In 1897 Galpin observed plants that were 8 feet tall. In 1949 Acocks noted that the plants were 4 ft. tall and locally fairly frequent. Road widening is now in progress in the pass and one

population near to the roadside had been eliminated. Miss Esterhuysen reports (verbal communication) that this species is still fairly plentiful higher up in the mountains between Tradouw Pass and Grootvadersbos. Flowering takes place from August to November. The large pink flowers and the presence of nectar indicate pollination by insects. Seed when ripe is ejected by the usual catapult mechanism and regeneration takes place from seed normally only after fires. The leaves have a sweet turpentine smell when crushed.

DISCUSSION

Having the staminode connate with the petal places this plant in the genus *Coleonema*. The following characters also contribute to exclude it from other genera of the Diosmeae: (1) *flowers* solitary, terminal or axillary, each with several basal bracts; (2) *petals* with an elevated groove enclosing the apex of the staminode, connate with the staminode below; (3) *anther* with a minute apical gland; (4) *disc* obvallate, narrow, exceeds the ovary; (5) *stigma* capitate; (6) *style* and *filaments* short, glabrous, erect; (7) *ovary* 5-carpellate.

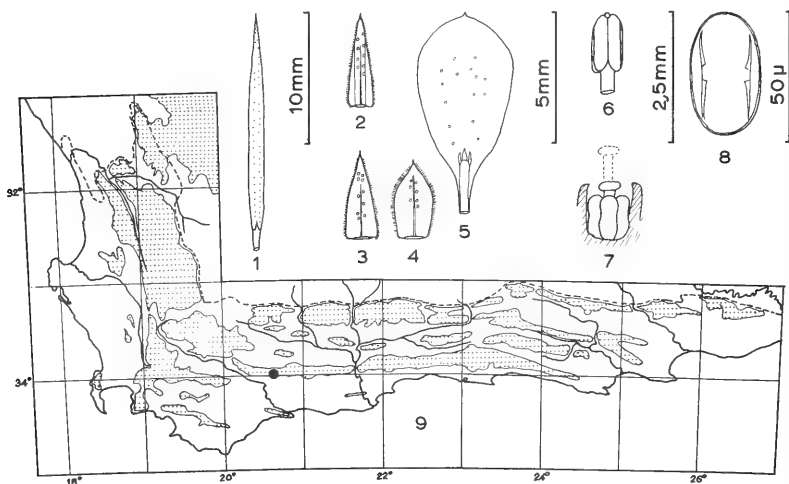


FIG. 15.

Coleonema pulchrum: 1, leaf. 2, uppermost bract. 3, bracteole. 4, calyx lobe. 5, petal with staminode. 6, anther. 7, gynoeceum and disc. 8, pollen. 9, distribution.

Coleonema pulchrum is a distinct species having linear leaves, up to 35 mm long and large pink flowers up to 13 mm diameter with many gland dots on the underside of the petals. It differs from *C. virgatum* which has smaller flowers without gland dots on the petals and leaves, also bracts and calyx lobes with more subulate apices. It differs from *C. pulchellum* and *C. aspalathoides* which

have shorter leaves and smaller flowers. All other species of *Coleonema* have white flowers.

IMPERFECTLY KNOWN SPECIES

Coleonema filiforme A.Juss. ex Don., Gard. and Bot. 1: 783 (1831) nom. nud. Type: *Diosma filiformis* D.C. herb. ex A.Juss. (P) = *C. pulchellum* Williams ?

Coleonema barosmoides Schltr. in Engl. Bot. Jb. 27: (1899) nom. nud. Type: unknown. = *C. aspalathoides* Juss. ex Don.?

SPECIES EXCLUDED

Diosma rubra L. Sp. Pl. 1: (1753). *Diosma foliis linearibus acutis glabris subtus bifariam punctatis*. Type: (LINN 240/4 as to right hand specimen only, lecto-type).

In a paper published by the author in 1974 the name *Diosma rubra* was rejected. However the recent publication of the revised *International Code of Botanical Nomenclature* adopted by the twelfth congress in 1975 has made it necessary to lectotypify this name. On the type sheet of *Diosma rubra* L. in London there are two specimens. On the left hand side is what is currently known as *Coleonema album* (Thunb.) Bartl. & Wendl. and on the right hand side is what is currently known as *Diosma hirsuta* L. It is clear therefore that Linnaeus' concept of his *Diosma rubra* was based on these two elements of which it is now necessary to choose one as a lectotype. As current usage in the past has tended to regard *Diosma rubra* L. as being a variety of *Diosma hirsuta* L., I therefore propose to choose the right-hand specimen on sheet 240/4 in the Linnaean herbarium as the lectotype of the name *Diosma rubra* L. This is a mature twig of a species already described as *Diosma hirsuta* L., bearing the characteristic fruits with petals persisting. The name *Diosma rubra* L. and the combination *Coleonema rubrum* (L.) Druce are consequently reduced to synonymy under *Diosma hirsuta* L.

Diosma ericoides L. Sp. Pl. 1: 198 (1753). *Diosma foliis lineari-lanceolatis subtus convexis bifariam imbricatis*. Type: Pluk. Phytogr. t.279, f.5 (1696), iconolectotype.

Under *Diosma* in the *Hortus Cliffortianus* (1737), Linnaeus described three species of which only the first was actually in cultivation in Clifford's garden. The second and third were based upon polynomials and figures in existing literature. In the *Species Plantarum* ed. 1 (1753) he divided the third species, *Diosma foliis setaceis acutis*, described in the *Hortus Cliffortianus*, into two parts, citing the first polynomial, i.e. *Diosma foliis setaceis acutis*, under his new *Diosma rubra* and the other polynomial, a direct quote from Plukenet, under the new *Diosma ericoides*.

A study of the material in Linnaeus' herbarium reveals that, at the time he published the *Species Plantarum* ed. 1 (1753), he had no dried plant material relating to *D. ericoides* in his possession (*vide* Dr T. T. Barnard, written communication). Under *D. ericoides* Linnaeus cited firstly "*Spiraea africana, ericae bacciferae foliis*. Raj. dendr.: 91" and secondly "*Ericaeformis, coridis folio, aethiopica, floribus pentapetalis in apicibus*." Pluk. Amalth.: 236, t.279, f.5."

With regard to the first polynomial, *Spiraea africana, ericae bacciferae foliis*, it is impossible to relate Ray's polynomial to any known plant and no specimen survives. However a very good description in Phillip Miller's *Figures of Plants* (1760) leaves no doubt in one's mind that he thought that it referred to *Coleonema album*. He even makes Linnaeus' description of *Diosma ericoides* appear to fit this plant.

The second polynomial, "*Ericaeformis . . . etc.*", refers to a figure in Plukenet's *Phytographia* t.279, f.5. The original specimen from which this drawing was made is preserved in the Sloane herbarium at the British Museum of Natural History and there can be no doubt that this plant is not *Coleonema album* but is a species of *Diosma*.

The diagnosis given by Linnaeus for his *D. ericoides* in the *Species Plantarum* (1753), "*DIOSMA foliis lineari-lanceolatis subtus convexis bifariam imbricatis*", cannot with certainty be attached to either of the above-mentioned plants, both of which have linear-lanceolate leaves. The words "*subtus convexis*" were plainly inserted to distinguish his description from any of the Ericaceae which often have leaves furrowed below and furthermore, neither plant, seeing that they possess alternate leaves, may be said to have leaves "imbricated in two rows".

Under the latest rules of nomenclature a type must be selected. As it is not known whether or not Linnaeus ever saw Plukenet's Herbarium, where the actual specimen upon which the figure cited by Linnaeus is preserved, the drawing fig. 5. on page 279 in Plukenet's *Phytographia* is chosen as the iconolectotype. The engraver has certainly made the plant look rather as if its leaves are imbricated in two rows as stated by Linnaeus in his diagnosis.

PHYTOGEOGRAPHY

An examination of the distribution maps relating to the various species in the genus *Coleonema* leaves one with the impression that we have a jigsaw puzzle in which some of the pieces are missing. Gaps and disjunctions are a feature of this genus. There are many mountains where no species of *Coleonema* have as yet been collected. The list is formidable: Piketberg, Riebeekskasteel, Paardeberg, Paarlberg, Southern Cedarberg, Cold Bokkeveld, Swarttruggens, Swartberg, Hex River Mountains, Anysberg, Touwsberg, Roodeberg, Kamanassie Mtns., Baviaanskloof Mtns., Cockscorn Mtns., Outeniquas, Tzitzikama Mtns., etc. There are also vast areas of sandy flats and coastal limestone where other genera

of the *Diosmeae* are found but as yet no species of *Coleonema*. None occur above an altitude of 1 400 m and, like other members of the *Diosmeae*, none are found growing on soils derived from the Malmesbury shales or from the Bokkeveld Series. In some species populations are found to be growing in isolated or severely restricted habitats such as: south slopes beneath small cliffs; amongst rocks on the T.M.S. outcrops; associated with silcrete-capped hills, etc.

Five species of *Coleonema* show distribution patterns with large disjunctions. In the case of the two more or less coastal species *C. album* and *C. pulchellum*, distribution might have taken place in former times during the various ice ages when the sea was at times at a much lower level and a suitable habitat lay exposed. The subsequent rise in sea level leaving the the outliers still surviving. Two other species *C. calycinum* and *C. aspalathoides*, which now occupy isolated and often restricted habitats, might have been widely spread when geological conditions were very different with vast areas between the mountain ranges still covered with silcrete peneplains derived from the erosion of the quartzitic mountain ranges. Subsequent erosion, perhaps due to the changes in the main river systems from east-west to north-south, isolated the populations from each other. If this is so it indicates the great age and endurance of these species. The main populations of *C. juniperinum* in the South West Cape consist of small, often diffuse, bushes rather soft to the touch. To the north, after a gap of 130 km, the plants are found to be quite large, stiff and almost prickly in a very much drier climate. No doubt high rainfall requirements have kept *C. nubigenum* confined to a fairly small area in the mountains of the South West Cape where it is none the less plentiful. The lack of success of *C. virgatum* and *C. pulchrum* in spreading much more widely along the Langeberg may seem strange until one considers the many other species that have relatively restricted distributions along the same range of mountains where, with the abundant rainfall, the competition must be very great.

Certainly the fact that *Coleonema* is absent from many areas is due largely to the small number of species in the genus. Here we are dealing with only eight out of a total of about 258 species in the *Diosmeae* a mere 3,1 %. Another reason may be that, in general, the plants require areas with a fairly high rainfall, peculiar habitats including possibly restricted altitude tolerances.

While agreeing that the small, slippery seeds after being ejected, may be transported short distances by ants, which may be able to grip and feed upon the aril, one simply cannot postulate any form of distribution over vast distances by any agency such as the wind or by birds. One is therefore forced to the conclusion that these species have been in existence for a very long time indeed.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the assistance and facilities made available to him at both the Bolus Herbarium with its invaluable library, at the Uni-

versity of Cape Town and the Compton Herbarium at Kirstenbosch. Loans of specimens have been made from and/or visits made to the following herbaria: B, BM, BOL, C, E, G, GRA, K, LINN, NBG, P, PH, PRE, S, SAM, UPS (abbreviated according to Lanjouw & Stafleu, 1964). The assistance received from these institutions is acknowledged with thanks. Special help in the elucidation of various problems has been received from Dr T. T. Barnard, Dr Peter Goldblatt, Dr Heino Heine and Dr J. P. Rourke and this is sincerely appreciated.

A NEW SPECIES OF *EUPHORBIA* FROM THE KAROO

L. C. LEACH*

ABSTRACT

A new tuberous rooted, succulent *Euphorbia*, *E. bruynsii* from the Karoo, is described.

UITTREKSEL

'n NUWE *EUPHORBIA* SOORT VANAF DIE KAROO

'n Nuwe sukkulente *Euphorbia* met 'n wortelknol, *E. bruynsii*, vanaf die Karoo, word beskryf.

Euphorbia bruynsii Leach, sp. nov. caule et ramis florentibus, foliis inflorescentia seminibusque illis *E. gariepinae* Boiss. aliquanto similibus et huic verosimiliter affinis sed radice tuberosa, caule singulo simplici vel sparsissime ramoso, cyathiis bisexualibus latissime divergens.

Typus: Cape Province, Steytlerville, *Bruyns 1814* (PRE, holo.; SRGH).

Planta perennis inermis succulenta, in aridis crescens ab fruticulis Compositarum et Mesembryanthearum bene protecta. *Radix* tuberosa sicyoidea, tubere sphaerica vel subcylindrico usque ad 35 mm diam. *Caulis* gracilis erectus, simplex vel sparsissime ramosus, ramificans fortasse tantum ubi laesus, laxe spiratim tuberculatus, aspectu aliquam flexuosus, dentibus conicis patentibus distantibus. *Folia* decidua, succulenta, glabra, sessilia vel breviter subpetiolata, basi aliquanto tumida, obovata, anguste obovata vel cuneato-elliptica, saepe acuta vel subapiculata, usque ad 15 mm longa, 3 mm lata, margine angustissime pellucideo, tuberculorum ad apicem exorientia, in partibus junioribus gemmam rubineam axillarem subtendens. *Inflorescentia* cymosa, terminalis, cymis simplicibus vel compositis e cyathio primo evolutis, plerumque dischysialibus interdum ramo tertio brevissime infra cyathium primum instructis, ramis ex axillis bractearum invicem evolutis, usque ad 30 mm longis, interdum denuo furcatis ramis tum brevioribus. *Cyathium* primum bisexuale, terminale, in pedicello usque ad 5 mm longo erecte portatum, bracteis binis ad folia similibus suffultum; cyathia sequentia similia sed bracteis minoribus. *Involucrum* cyathiforme usque ad 5 mm longum, 3–4 mm diam. glandulis inclusis, intus dense villosum, extus glabrum.

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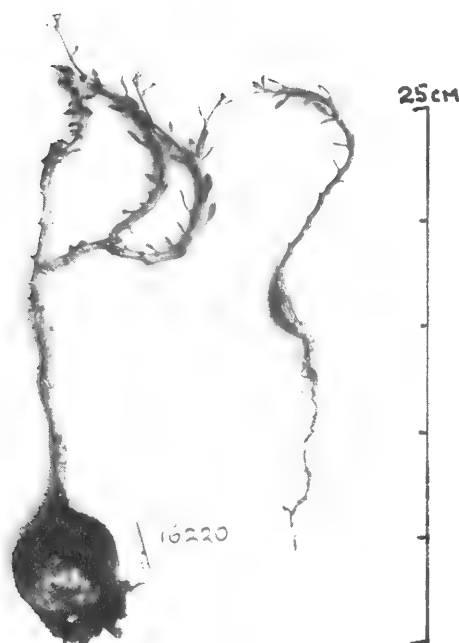


FIG. 1.

Euphorbia bruynsii Leach. Plants from Steytlerville, Bruyns 1814.

viride versus apicem rubescens, tandem flavescens; *glandulis* 5, transverse reniformi-oblongis, usque ad $1,4 \text{ mm} \times 0,6 \text{ mm}$, superficie leviter convexa, foveolata nectare copioso, olivacea, rubiginoso-marginata, denique omnino fusco-rubiginosa; *lobis* 5, subquadratis, fimbriatis, utrinque dense albi-villosis, c. $0,75 \text{ mm}$ longis. *Flores masculi* pedicellis $\pm 2,5 \text{ mm}$ longis, albis sparse pubescentibus; filamentis subroseis, $1-1,25 \text{ mm}$ longis glabris; antherae eburneae, polline dilute aurantiaco; bracteolis filamentosis villosis, c. $3,5 \text{ mm}$ longis. *Flos femineus* glaber, pedicello c. 3 mm longo; styli dilute rosei, in columnam ad medium connati, supra libri, patuli reflexique, brevissime bilobati lobis lateraliter divergentibus, luteolis subtranslucentibus. *Capsula* 3-lobata, glabra, cremea, plus minusve late ovoidea, c. 6 mm diam., 4 mm alta, ex involucri breviter exserta, pedicello crasso, $4,5-5 \text{ mm}$ longo, c. 1 mm diam. *Semen* plus minusve ovoideum, ad apicem acutum, basi truncatum, lateraliter obtuse angulatum,

subtiliter farinosum, cremeum, versus basim pallide brunnescens; sutura leviter prominens.



FIG. 2.

Left: Inflorescence, *Bruyns 1814*, cult. SRGH. Right: Portion of stem showing spirally arranged tubercles and leaves.

Plant: an unarmed succulent perennial with a spherical or subcylindric tuberous root up to 35 mm diam., and long underground stem or neck. *Stem* slender, erect, the above ground portion simple or very sparingly branched (branching possibly only when damaged), laxly spirally tuberculate with spreading conical teeth, the distant teeth imparting a somewhat flexuose appearance to the stem. *Leaves* deciduous, succulent, glabrous, sessile or shortly subpetiolate, somewhat swollen at the base, obovate, narrowly obovate or cuneate-elliptic, often acute or subapiculate, with a very narrow pellucid margin, up to 15 mm long, 3 mm wide, arising from the apex of the tubercles, on young parts usually subtending a ruby axillary bud. *Inflorescence* cymose, usually dischiasial, developing from an initial, terminal, pedicellate, bisexual cyathium; pedicel up to 5 mm long, supported by paired bracts similar to the leaves; cyme branches developing successively from the axils of the bracts, up to 30 mm long, becoming shorter with successive forkings, each bearing paired bracts and a shortly pedicellate, bisexual cyathium, similar in all respects to the initial cyathium; a third branch subtended by a similar bract, is sometimes developed from very

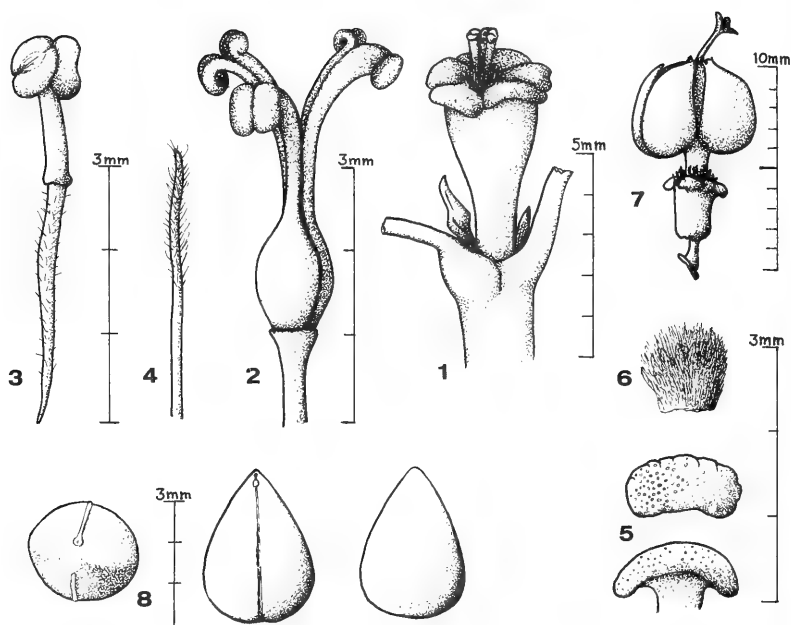


FIG. 3.

1. Cyathium, *Euphorbia bruynsii*; 2. Female flower; 3. Male flower and 4. bracteole; 5. Involucral gland; 6. Involucral lobe; 7. Cyathium in fruit; 8. Seed.

shortly below the paired bracts of the initial cyme. *Involucre* deeply cup-shaped up to 5 mm long, 3–4 mm diam. including the glands, densely hairy inside, outside glabrous, green, reddish towards the apex and eventually becoming yellowish; *glands* 5, transversely oblong-reniform, up to 1,4 mm × 0,6 mm, slightly convex on the pitted upper surface, with copious nectar, green with brown-red recurved margins, eventually becoming entirely red-brown; *lobes* 5, subquadrate, fimbriate, densely white hairy on both sides, ±0,75 mm long. *Male flowers* with white, sparsely pubescent pedicels ±2,5 mm long; *filaments* faintly pink, glabrous, 1–1,25 mm long; anther thecae cream becoming yellowish, pollen yellow-orange; bracteoles filamentous, villous, ±3,5 mm long. *Female flower* glabrous, erect on a pedicel ±2 mm long; *styles* ±3 mm long, united in a column for about half their length, free above, laterally compressed with a deep ventral groove, spreading recurved with the enlarged apex very shortly bilobed, the pale yellow somewhat translucent lobes widely laterally divergent. *Capsule* 3-lobed, glabrous, cream, more or less broadly ovoid, ±6 mm diam., 4 mm high, shortly

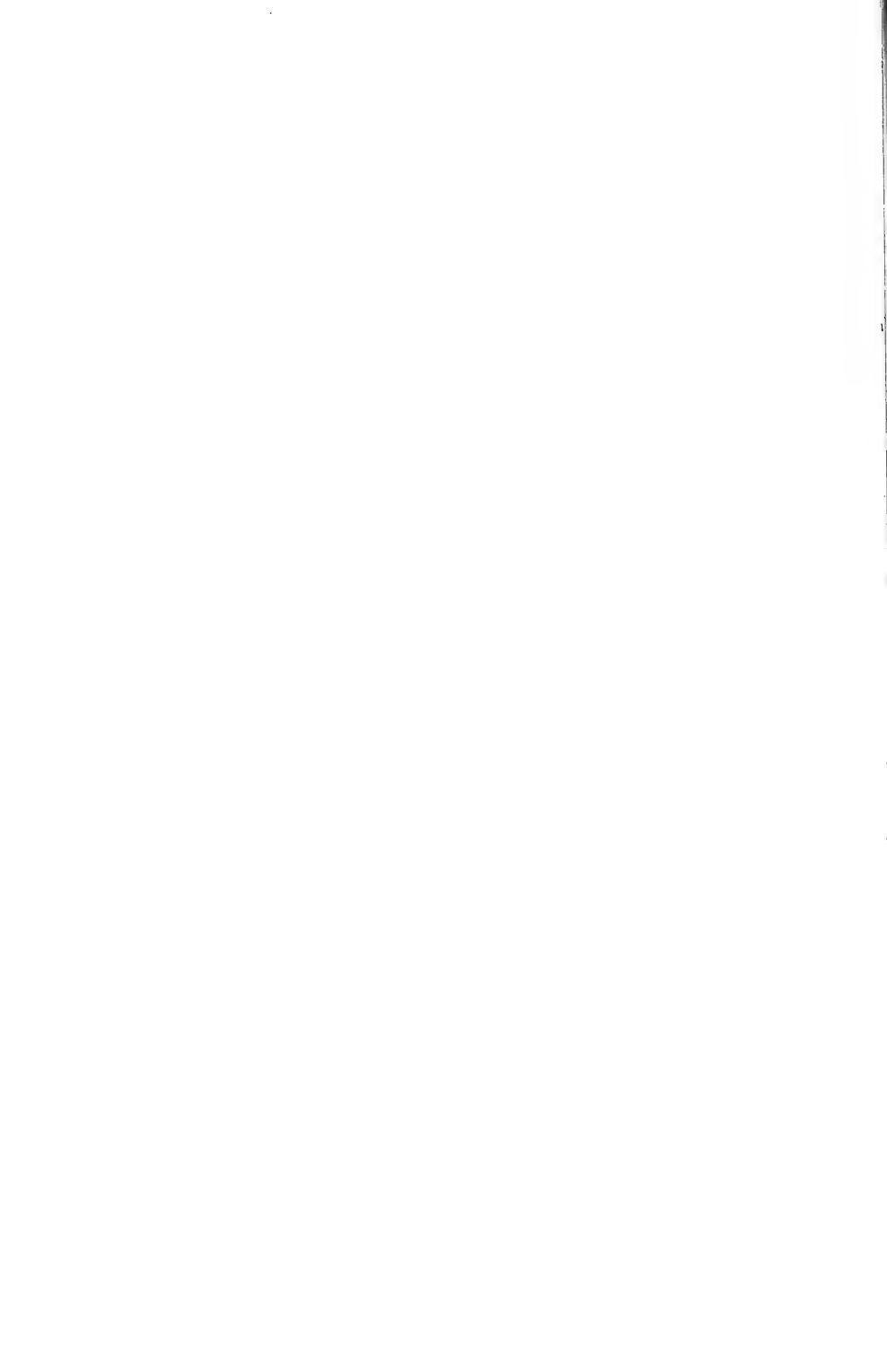
exserted from the involucre on a stout pedicel, 4.5–5 mm long, ± 1 mm diam. *Seed* more or less ovoid, acute at the apex, more or less truncate at the base, somewhat obscurely obtuse-angled at the sides, smooth, finely farinose, cream shading to brownish towards the base, with a slightly raised suture.

CAPE PROVINCE—3324 (Steytlerville): small conglomerate hill east of Steytleville (-AD), plants in association with and supported by small shrubs (Compositae and Mesembryanthemaceae), Nov. 1978, *Bruyns 1814* (PRE, holo.: SRGH).

The description of this interesting new species is based on the two plants in cultivation at the National Herbarium, Salisbury, together with the notes given to me by the collector, Peter Bruyns, after whom the species is now named and whose collections in Cape Province have brought to light several new taxa.

The new species does not appear to be very closely related to any of its geographically associated congeners; the stem is reminiscent of the unnaturally elongated branches which sometimes develop under cultivation in specimens of *E. tridentata* Lam., but there the resemblance ends. Its nearest relationship appears probably to lie with *E. gariepina* Boiss. with which it shares the somewhat tessellately oblong-marked, conically tuberculate stems and branches. It is in leaf and inflorescence characters, however, that *E. bruynsii* is closest to *E. gariepina*, with its very similar succulent leaves and a terminal inflorescence which differs materially only in its bisexual character, while most significantly the seeds are almost identical. However, the new species differs considerably from its densely branched more succulent relative in being a small tuberous rooted plant with a single, slender, usually simple stem.

E. bruynsii is known only from the type locality near Steytleville where plants, which are by no means common, are to be found growing in the protection of and with the support of small shrubs on a low conglomerate hill (Bruyns).



**AN INTERESTING NEW SPECIES OF *PERSEA* MILLER (LAURACEAE)
FROM THE KADOORIE BOTANIC GARDENS, NEW TERRITORIES, HONG
KONG***

A. J. G. H. KOSTERMANS**

ABSTRACT

A new species, *Persea kadooriei* Kostermans from Hong Kong, is described.

UITTREKSEL

'N INTERESSANTE NUWE *PERSEA* MILLER (LAURACEAE) SOORT VANAF
DIE KADOORIE- BOTANIESE TUINE, NEW TERRITORIES, HONG KONG

'n Nuwe soort, *Persea kadooriei* Kostermans vanaf Hong Kong, word beskryf.

INTRODUCTION

In March, 1972, Mrs. G. Barretto had for some months been employed in the Kadoorie Botanic Gardens, Hong Kong. Although not a botanist by profession, she is a plant lover and gardener. At that time Dr. S. Y. Hu of the Arnold Arboretum, U.S.A., was gathering material for a revised *Flora of Hong Kong*, and Mrs. Barretto, with many others, assisted her in obtaining the necessary material. It happened that in that spring of 1972, almost every tree of *Persea* in the Kadoorie Gardens (60—80 trees) was in flower. Material was collected and presented to Dr. Hu.

On 26 August, 1972, Dr. Hu wrote that she thought there were two new varieties and one new species of *Machilus* (= *Persea*) represented in the material. She wrote that the new species might be *Machilus levinei* (= *Persea levinei* (Merr.) Kosterm.), but she later reconsidered this and thought that the species was undescribed.

Mrs. Barretto continued to observe the *Persea* trees in the Gardens, especially those assumed to represent an undescribed species. These trees flowered again in 1977, a span of five years from the last time. Apart from collecting essential parts, she also had colour photographs taken of the trees, the flowers.

*The Editor-in-Chief acknowledges with gratitude the assistance of Mr Horace Kadoorie who has borne the cost of the publication of this paper. Mr Kadoorie has for many years been a patron to young scientists and he has long had links with the National Botanic Gardens of South Africa at Kirstenbosch.

***Hoc tempore* visiting professor, Department of Botany, University of Peradeniya, Sri Lanka.

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and the fruit, and noted down essential characters. The trees did not flower in 1978, or in 1979, or 1980; they are likely to flower every five years only.

In April, 1978, Dr. Hu revisited Hong Kong; she suggested to Mrs. Barretto that the matter should be referred to me.

All available material was then sent to me in Peradeniya in Sri Lanka.

Rarely has a species been provided with so much documentary information. Mrs. Barretto was assisted by Mark Williams who collected, recorded and photographed specimens and sketched flower details. The drawings were prepared by Teresa Tung and Pauline Lai. Y. W. Tang also supplied photographs.

As I had no herbarium material for comparison at my disposal in Peradeniya, I requested Dr. J. F. Veldkamp of the Rijksherbarium, Leiden, Netherlands, to compare the materials of the new *Persea* with *Persea fructifera* Kosterm. (= *Machilus edulis* King ex Hooker f.) and *P. robusta* (W.W.Sm.) Kosterm. (= *Machilus robusta* W.W.Sm.), to which it seemed allied, and Mrs. Barretto to provide me with a description of *Persea liangkhwangensis* (Chun) Kosterm. (= *Machilus liangkhwangensis* Chun), another relative.

For their co-operation, I express my sincere thanks.

***Persea kadooriei* Kosterm., sp. nov. (Figs 1–12)**

Arbor mediocris, ramulis crassis, innovationibus multi-perulatis, longe conicus, partibus medianus dense minute sericeis, apicalibus glabris, apice minutissime dense sericeis exceptis, foliis chartaceis vel subcoriaceis glabris oblanceolatis usque ad subobovato-oblongis, apice breve late acuminatis, basin versus sensim attenuatis, supra perdense et laeviter areolatis, nervo mediano impressis, lateraliter areolis quadrangularis munitis, nervis lateralibus vix prominulis, subtus perdense minute reticulatis, glaucis, nervo mediano valde prominentibus, nervis lateralibus 18–23 paribus tenuibus prominentibus erecto-patentibus vel subpatentibus marginem versus arcuatis, nervis secundariis obscuris parallelis, petiolis sat gracilibus longis supra concavis; paniculis pseudo terminalibus aggregatis glabris foliis multo minoribus sat paucifloris, pedunculis communis crassis albis (in vivo), ramulis paucis brevibus; pedicellis longis sat tenuibus, apicem versus incrassatis; tubus calycinus nullis, hypanthium intus minutissime pubescentibus; tepalis oblongis vel subobovato-oblongis, tribus exterioribus glabris, fimbriatis; tribus interioribus utrinque sparse minutissime sericeis; filamentis longis, basis versus sub-incrassatis, pilosis; glandulis sat magnis longe stipitatis; staminodiis longe stipitatis, anguste subcordatis acutis, ovario glabro, cylindrico; stylo filamentis aequilongis, stigmate obscuris lateralibus; fructus depresso-subglobosis nigris (in vivo), tepaliibus non incrassatis adpressis.

Typus: Hong Kong, New Territories, *G. Barretto s.n.* (L); *G. Barretto s.n.* (HK Herbm., isotypus).



FIG. 1.

Persea kadooriei. A. The habit sketch of a flowering branch showing the aggregate peduncles, the prominent lower and upper bud-scales, the flower buds, and some flowers; also shown is a leaf, with detail of venation. B. A flower, showing the tepals, the stamens, the latrorse and introrse anthers, and the glands.

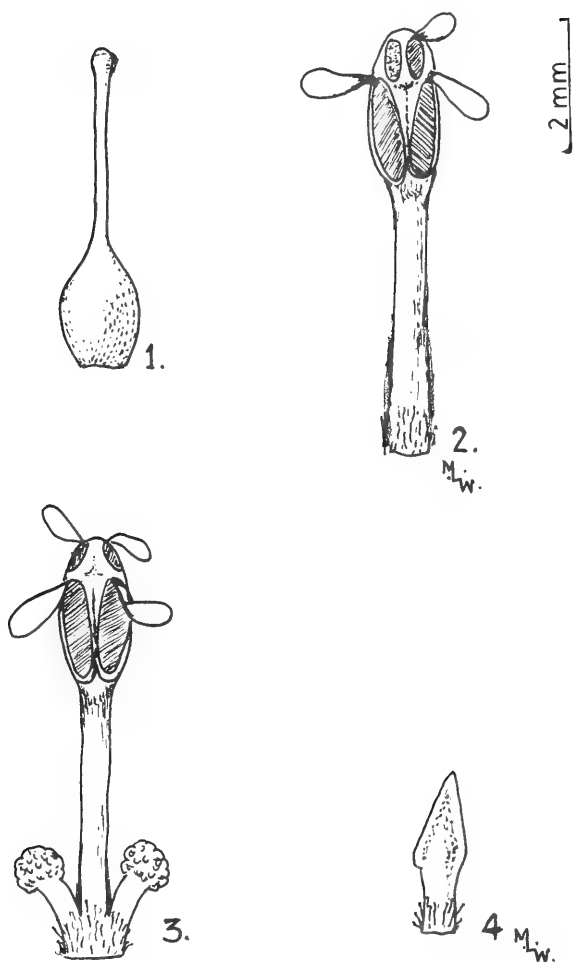
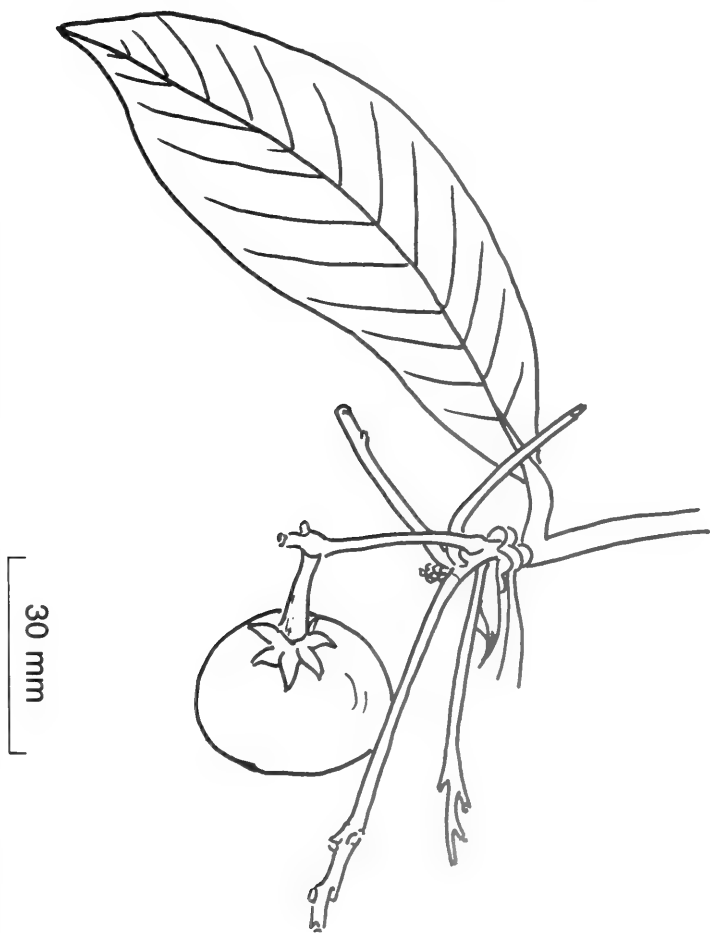


FIG. 2.

Persea kadooriei. Detail:—1. Flask-shaped ovary and the style. 2. A stamen, the valvate anthers introse, the base short pilose. 3. A stamen, the valvate anthers latrorse, the glands and slightly pilose base. 4. A staminode, the base hairy on inner side.



PAULINE LAI

FIG. 3.
Persea kadooriei. A fruit-bearing branch, showing the globose fruit, with the persistent tepals adpressed to the base.



FIG. 4.

Persea kadooriei in full bloom, the flowers overall creamy white, March, 1977. (Tree K.5/1).



FIG. 5.

Leafy branch bearing a terminal cluster of flower buds.



FIG. 6.

A cluster of flower buds, showing the prominent upper sheathing bracts.



FIG. 7.

Close-up of a panicle of buds and opening flowers showing the glabrous branches extending from the stout peduncle, and the short flower-bearing ones.



FIG. 8.

A young leafy shoot showing the lower and upper forms of imbricate scales.



FIG. 9.

A vigorous leafy shoot, showing the young leaves, red-brown, and very tender. Note the large protective imbricating scales, broad ones at the base, the long ones above. (Tree K.5/3).



FIG. 10.

The trunk of *Persea kadooriei*. Note the bark in shades of pale to medium brown, and the raised pieces of corky lenticels. (Tree K.5/1).



FIG. 11.

Close-up of Fig. 10, showing the corky lenticels and the small sections of bark that fall away in bits.



FIG. 12.

A branch bearing semi-ripe and ripe globose fruit.

Tree, up to 10 m tall, bole 406 mm diameter at c. 1 m height. *Bark* rather smooth, brownish, peeling off in small pieces, with corky lenticels, which are also present on the larger, horizontal branches and on smaller branches. *Crown* rounded. Ultimate flower-bearing branchlets thick, with large, round leaf scars. The flush protected by numerous large protective scales (reduced leaves), forming in spring a slender cone of scales, up to 90 mm long, and 15 mm diameter at the rounded base, the lowest ones thick (with thin marginal part) sub-orbicular, up to 8 mm wide and 5 mm high, apiculate; the ones developing in spring from orbicular (lower) ones, c. 10×15 mm, densely minutely sericeous and fimbriate to the apical, obovate-oblong, 20×35 mm long ones, which are only sericeous at the apical part, these are also much thinner. *Mature leaves* glabrous, chartaceous to sub-chartaceous, oblanceolate to subobovate-oblong, 100×240 mm— 110×330 mm (mostly 80×270 mm), shortly acuminate (acumen broad, 10–20 mm long) gradually tapered towards the base; above densely, very minutely, smoothly areolate, glossy, along the midrib (and faintly along the ribs) with deep sub-quadrangular pittings, midrib slightly impressed, yellowish (fresh) like the slender, hardly-raised lateral nerves; below pale green to glaucous (fresh), densely, very minutely reticulate; midrib stout, strongly prominent, lateral nerves slender, prominent, erect-patent to more patent, 18–23 pairs, towards the

margin arcuate and slightly ascendent; in between a short accessory lateral nerve (some lateral nerves are forked); secondary nerves thin, perpendicular to the lateral nerves, a number perpendicular to the midrib. *Petiole* relatively thick, 15–25 mm long, concave or flattish above. *Leaves* aggregate; young leaves red-dish-brown with a tuft of hairs apically.

Panicles aggregate, glabrous, pseudo-terminal, initially covered by large, rather fleshy, sub-quadrangular, 15×15 mm (lower ones) to obovate-elliptic, 5×25 mm (upper ones) bud-scales, densely, very minutely sericeous outside. *Main peduncles* stout, white (fresh), up to 80 mm long, bearing well-spaced, rather few, up to 15 mm long branches, which in turn bear very short branches with 1–3 flowers. *Flowers* 11–12 mm (occasionally 14 mm) diameter, scented, the back creamy-green, the front ivory-white. *Bracts* long, slender, 10 mm (lower) to 3 mm (upper ones). *Pedicels* 10 mm long, thickish (after drying, thin), the apical part under the hypanthium elongate cup-like, glabrous, distinct, filled with loose parenchymatous tissue. *Calyx tube* none. *Hypanthium* inside slightly white-pubescent. *Tepals* oblong to subobovate-oblong (becoming very narrow after drying) 5–6.5 mm long, 2–3 mm wide; outer three glabrous, fimbriate; inner three somewhat sericeous both sides and fimbriate. *Filaments* 4 mm long, rather thickish (thin after drying), towards their base slightly thickened and with a few short thin hairs; anthers oval, 1–1.5 mm long, of the inner three erect, stamens latrorse; of the outer series erect-patent stamens, introrse. *Staminodes* 2 mm long, the filament slightly more than 1 mm, the base hairy on inner side, glabrous on outside, the head narrowly triangular, acute. *Glands* ellipsoid, rather large, on slightly pilose, 1 mm long stipes. *Ovary* glabrous, flask-shaped. Style 2.5 mm long; stigma inconspicuous, lateral. *Fruit* globose or depressed-globose, up to 25–30 mm diameter, at maturity black with dark bluish bloom; the not enlarged tepals horizontal, adpressed to the base of the fruit.

Distribution: Hong Kong, New Territories, alt. c. 500 m.

MATERIALS EXAMINED

HONG KONG, New Territories: growing in nature within Kadoorie Botanic Gardens, alt. c. 500 m. north-facing rocky mountainside. Trees K.5, K.5(1), and K.5(3), March: flowering, and July: fruit. *Mrs G. Barretto s.n.* (L); same K.5 tree, fl. *S.Y. Hu 11510* (A).

NOTES

The species is related to *Persea fructifera* Kosterm. and *P. robusta* (W.W.Sm.) Kosterm., but differs by the venation, leaf and flower size, indumentum, and the much smaller fruit.

This handsome new *Persea* species is named in honour of Mr Horace Kadoorie.

The Kadoorie family is known for philanthropy and benevolence in the spheres of education, agriculture, and social welfare in Hong Kong and other parts of the world.

A NEW SPECIES OF *LEUCADENDRON* (PROTEACEAE) FROM THE OUTENIQUA MOUNTAINS*

ION WILLIAMS

(Honorary Reader, Bolus Herbarium, University of Cape Town
Honorary Research Worker, Compton Herbarium, Kirstenbosch)

ABSTRACT

A very distinct new species of *Leucadendron* is described for the first time.

UITTREKSEL

'N NUWE SOORT *LEUCADENDRON* (PROTEACEAE) VANAF DIE OUTENIEKWABERGE

'n Nuwe baie duidelik onderskeibare *Leucadendron* soort word vir die eerste maal beskryf.

Leucadendron olens Williams, sp. nov. propria propter monomorphophylla, inflorescentiam maris 9 mm diam. auream fragrantem, inflorescentiam feminae 5 mm diam. ad apice bi-, tri-floriferam.

Frutex 1,2 m altus, monocaulis, rectus. *Rami* recti, pauci, glabrescenti, rubelli. *Ramuli* fasciculati, graciles sparsim puberuli. *Folia* 7-11 mm longa, 1,2-2 mm lata, lineari-lanceolata, acuta, mucronata, glabra, coriacea, initio sparsim villosa-ciliata, alterna, adpresso-erecta, incurva. *Inflorescentia* maris 9 mm longa, 8 mm diam., solitaria, terminalia, flava, valde suaveolens. *Bractae basales* varians, 4,2 mm longae, 3,3 mm latae, ovatae, glabrae, ciliatae. *Bracteola* 5 mm longa, 1,2 mm lata, lineari-spathulata, ciliata, costa villosa. *Tubus perianthii* 4 mm longus, crispo-pubescent, stylo connato. *Unguis* 1,7 mm longus, pubescens. *Limbus* 1,7 mm longus, linearis, glabrescent. *Anthera* 1 mm longa, linearis, mox sine pollen. *Pollen* 42 μ diam., siccus. *Stigma abortivum* 1,5 mm longum, clavatum, bifidum. *Stylus* 2 mm longus, filiformis, glaber, deflexus. *Squamae hypogynae* nullae. *Receptaculum* 1,8 mm diam., globosum. *Inflorescentia feminae* 5 mm diam., solitaria, terminalia conico-ovoidea, acuta, bi-, tri-florifera. *Bractae basales* varians, 6 mm longae, 6 mm latae, deltoideae, sub-acutae, glabrae, ciliolatae. *Bracteola* 5,8-6 mm longa, 1,8-2,8 mm lata, elliptica, obtusa, \pm glabra, ciliata. *Tubus perianthii* 5 mm longus, in super villosus, in medio connatus, ad basim glaber. *Unguis* 4 mm longus, pubescens. *Limbus* 1,5 mm longus, pubescens. *Staminodium* 0,5 mm longum, lineare, decumbens. *Stigma* 0,9 mm lon-

*The Editor-in-Chief acknowledges with gratitude the financial assistance of Dr Ion Williams with the colour reproduction of Figure 1.

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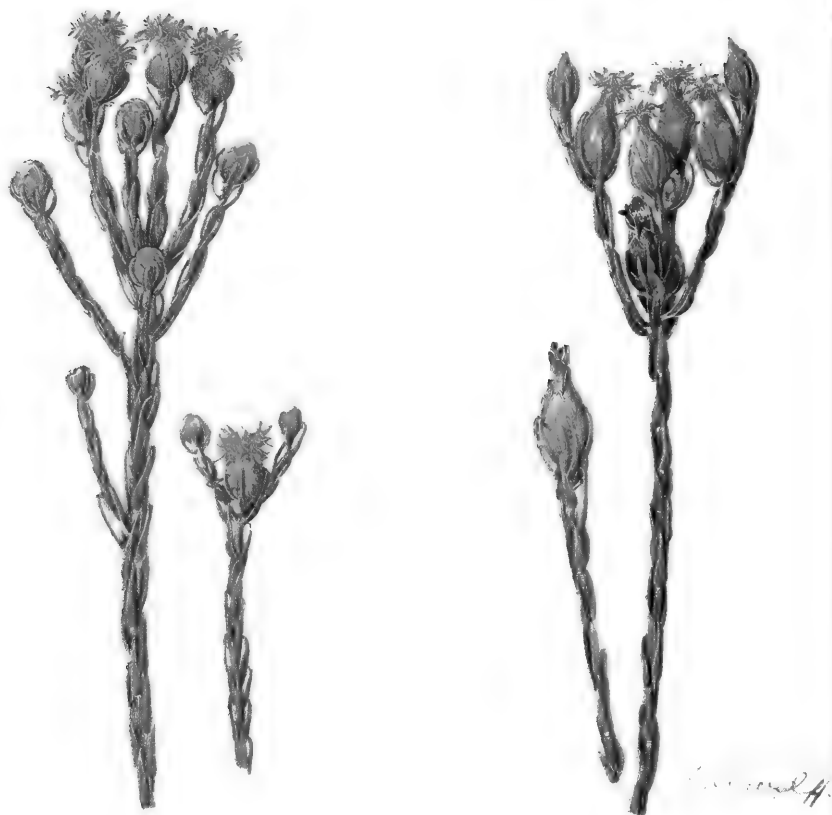


FIG. 1
Leucadendron olens Williams. Male (left) and female (right) branches.



(1) male inflorescence ($\times 3$); (2) male flower ($\times 5$); (3) basal bract ($\times 4$); cross section through male inflorescence; (5) male floral bract ($\times 2$); (6) female inflorescence ($\times 3$); (7) female flower ($\times 3$); (8) gynoecium ($\times 3$); (9) basal bract ($\times 2$); (10) cross-section through female inflorescence ($\times 3$); (11) female floral bract ($\times 2$); (12) fruit ($\times 3$).

gum, 1,2 mm latum, bifidum. *Stylus* 7,5 mm longus, filiformis, rectus, glaber. *Ovarium* 1,4 mm longum, 1,2 mm diam., globosum, ad apice dense villosum. *Squamae hypogynae* nullae. *Receptaculum* 2 mm diam., globosum. *Strobilus maturus* 17 mm longus, 8 mm diam., conico-ovoideus, glaber. *Nux* 5,5 mm longa, 2,2 mm lata, villosa apicem versus.

Type: CAPE—3322 (Oudtshoorn): Modderasskloof, north side of the Outeniqua Mountains, George Division (-CD), 590 m (1950 ft.) alt., 25/6/1980, *Williams 3031* (NBG, holotype; K, PRE, BOL, STE, S, MD, M, isotypes).

Shrubs about 1,2 m tall, erect, with a reddish hue, single stemmed at base. *Branches* erect, rod-like, thinly adpressed pubescent becoming glabrescent, reddened, leaves persisting. *Branchlets* clustered, slender, erect, thinly adpressed pubescent, partly hidden by the leaves. *Leaves* similar in both sexes, 7–11 mm long, 1,2–2 mm broad, linear-lanceolate, acute, mucronate, glabrous, coriaceous, sparsely villous-ciliate at first, alternate, adpressed erect, incurved. *Male inflorescence* 9 mm long, 8 mm diam., solitary, terminal, globose, yellow, very sweetly scented. *Involucral leaves* not conspicuous, similar to the stem leaves, about 5 in number. *Basal bracts* varying in size, one measured 4,2 mm long, 3,3 mm broad, concave, ovate, ciliate, glabrous. *Floral bract* 5 mm long, 1,2 mm broad, linear-spathulate, ciliate above but not at the apex, midrib villous. *Perianth tube* 4 mm long, crisped pubescent, connate with the style. *No hypogynous scales*. *Claw* c. 1,7 mm long, pubescent, recurved, connate with the filament. *Limb* 1,7 mm long, linear, glabrous towards the apex. *Anther* 1 mm long, linear, soon devoid of pollen. *Pollen* triangular with pores at the apices and sides 42 μ long, not sticky. *Stigma* abortive, 1,5 mm long, clavate, minutely bifid, does not act as a pollen presenter. *Style* 2 mm long, filiform, becoming deflexed, connate with the perianth tube below. *Male bud* 6,5 mm long, somewhat thickened above, apex glabrous, densely crisped pubescent below. *Receptacle* 1,8 mm diam., globose. *Female inflorescence* 5 mm diam., solitary, terminal, conic-ovoid, glabrous, surrounded by a few narrow involucral leaves with 2 or 3 yellow flowers projecting at the apex showing their large bifid stigmas. *Basal bracts* numerous, varying in size, one measured 6 mm long, 6 mm broad at base, deltoid, sub-acute, ciliolate, glabrous. *Floral bract* 5,8–6 mm long, 1,8–2,8 mm broad, elliptic, obtuse, ciliate, glabrous except for a few long silky hairs, standing in a tuft of long silky hairs at the base. To either side are to be found long narrow pubescent sterile bracts. *Perianth tube* 5 mm long, villous above, glabrous below, connate in the middle. *Claw* 4 mm long, pubescent, recurved more than 180°. *Limb* 1,5 mm long, lanceolate-obtuse, pubescent, apex hooked in. *Staminodes* 0,5 mm long, linear, decumbent. *Stigma* 0,9 mm long, 1,2 mm broad, bifid, edges revolute. *Style* 7,5 mm long, filiform, erect, glabrous. *Ovary* 1,4 mm long, 1,2 mm diam., globose, densely clothed in the upper half with long

silky hairs. *No hypogynous scales.* Fruit a cone 17 mm long, 8 mm diam., conic-ovoid, glabrous with the bracts red-tipped, 2 or 3 seeds ripening in each fruit. Seed a hard nutlet 5.5 mm long, tufted at the apex making it 8.5 mm overall, 2.2 mm broad, becoming 4-ribbed and glabrous at the base.

As far as is known this species had not been collected until the author and his family came across it by accident whilst examining a population of *Leucadendron ericifolium* along the forestry track in an area known as Modderasskloof on the north side of the Outeniqua Mountains to the west of the farm Waboomskraal near George. The whole area for many kilometres is overrun with *Hakea sericea* which is a very serious threat to the indigenous vegetation. Immediate action by the Department of Forestry will be required if this very interesting and unique new *Leucadendron* is to be preserved. There is no other species of *Leucadendron* which has flowers as sweet smelling as those of the male *L. olens*. In fact it can rank on a par with those other species of sweet-smelling flowers whose perfume will pervade a whole room.

In 1972 when a monograph on *Leucadendron* was published, the species *L. ericifolium* was thought to be extinct. Since then however it has been discovered growing on the Rooiberg in the Little Karoo to the north of the Langeberg and all along the north side of the Attaquas and Outeniqua mountains between the Gouritz River and George.

SPECIMENS EXAMINED

Type only. As above.

DISTRIBUTION, BIOLOGY AND VARIATION

As far as is known *L. olens* is found growing only along the north slopes of the Outeniqua Mountains between the headwaters of the Groot Doring and Klein Doring rivers over a distance of about 4 km at altitudes of from 590 to 790 m above sea level. It grows upon dry stony gravelly slopes derived from the Table Mountain Sandstone, the surface often strewn with blackish stones. The yellow flowering male plants are quite conspicuous when in bloom.

Of all species of *Leucadendron*, *L. olens* is most closely related to *L. ericifolium* R.Br. but appears to be somewhat less specialised. Both plants would seem to be anemophilous neither having hypogynous scales and therefore no nectar to attract insects. In both cases the pollen is not sticky and can be dispersed by the wind. The abortive stigma in the male does not act as a pollen presenter. In both species the female stigma is very large and protrudes prominently. However the male inflorescence in *L. olens* being larger and possessing many more flowers is not as much reduced as in *L. ericifolium*. It does, none the less, still retain the ability to produce a very fragrant perfume which may be a survival from the time when the species was pollinated by insects. In *L. olens* the num-

ber of flowers in the female head is about three but in *L. ericifolium* this has been reduced to only one. In *L. olens* all leaves are similar in shape but in *L. ericifolium* one finds ericoid leaves towards the base of the plant and flattish linear leaves above that are considerably smaller in the male plants.

No significant variation had been noted in those populations of *L. olens* that have been examined but one or two putative hybrids with *L. ericifolium* have been seen (Williams 3028). These show characters which are intermediate between those of the putative parent species. These putative hybrids bear slender branchlets with ericoid leaves towards the base of the plant as in *L. ericifolium*, a character not seen in *L. olens*.

PUTATIVE HYBRIDS

L. ericifolium R.Br. \times *L. olens* Williams, male and female.

CAPE—3322 (Oudtshoorn): Modderasskloof, north side of the Outeniqua Mountains, George Division (-CD), 590 m alt., 15/7/1980, Williams 3028 (NBG, BOL, PRE).

DISCUSSION

In the arrangement of species adopted in the *Revision of the Genus Leucadendron* (Williams, 1972), *L. olens* with its nut-like seed should be placed in the section *Leucadendron*, sub-section *Uniflora*.

Leucadendron olens is recognised as a distinct species having monomorphic leaves, the male flower head 9 mm in diam., bright yellow and fragrant and with the female head 5 mm in diam., conic-ovoid, glabrous with 2 or 3 flowers at the apex. It differs from *L. ericifolium* which is a much taller plant with dimorphic leaves having very small and numerous male heads and silvery pubescent female heads bearing only one flower at the apex. The name refers to the fragrant flowers of the male plant.

REFERENCE

- WILLIAMS, Ion J. M., 1972. A Revision of the Genus *Leucadendron* (Proteaceae). *Contr. Bol. Herb.* 3: 105

BOOK REVIEWS

REPRODUCTION IN FLOWERING PLANTS, edited by Dr Q. W. Ruscoe in *New Zealand Journal of Botany*, volume 17 (4), with pp. 260 (425-685). Wellington: Science Information Division, DSIR, 1979.

This volume contains invited review papers read at the International Symposium on Reproduction in Flowering Plants. This symposium was held in Christchurch, New Zealand in February 1979 and was organised under the auspices of the Royal Society of New Zealand and sponsored by the International Union of Biological Sciences.

Reproduction in flowering plants is, in spite of its vital importance, an orphan in South African botany and this publication must be seen as a very welcome and timely one.

The volume starts off with Professor Herbert G. Baker's (not the Herbert Baker of the Union Building fame) very interesting banquet address on a "slightly irreverent" topic, "Anthecology: Old Testament, New Testament, Apocrypha". The review papers cover a wide spectrum of flower biology and several concepts are dealt with such as birds as pollinators, other pollination agents, pollination mechanisms, pollen-stigma interaction, heterostyly, incompatibility, starch in pollen grains, breeding systems in trees and grasses, paraxial reproduction, genetic recombination and embryology.

Although not of the same standard, the authors are all specialists in their respective fields, which makes this volume a compilation of very valuable information. Every paper is supported by an extensive list of references which will be of great value to students in reproduction biology.

P. J. ROBERTSE

ADVANCES IN RESEARCH AND TECHNOLOGY OF SEEDS, Part 4, edited by J. R. Thomson, with p. 111. Wageningen: Centre for Agricultural Publishing and Documentation, 1979. 150 × 225 mm paperback Dfl. 27, 50.

Advances in Research and Technology of Seeds is a successor to the *International Seed Testing Association Seed Bibliography*. Its purpose is to publish reviews on recent literature covering studies on all the various aspects of seed. It is primarily aimed at research workers.

This fourth number includes reviews on weed seeds (H. Kolk, Sweden), seed deterioration and loss of viability (E. H. Roberts, U.K.), germination of seed (M. E. H. Johnston, New Zealand) and pelleting and other presowing treatments (J. H. B. Tonkin, U.K.).

The review on weed seeds covers 82 papers published between 1972 and 1977. Various topics such as weed seed production, chemical composition, dissemination, germination behaviour, influence of external and internal factors on germination, longevity and the effects of herbicides on viability are reviewed.

In his contribution on seed deterioration and loss of viability studies (125 papers 1972-1978), Roberts has expertly and critically reviewed the important papers in this field. The review concerns mainly aspects which are today of fundamental academic interest. However, attention has also been paid to some investigations of applied nature. Although the principles of storing orthodox seed are now fairly well established it is pointed out that little progress has been made with the storage of recalcitrant seeds. This category includes the seeds of many tree species.

The third review in this publication covers a wide array of topics (277 papers 1975-1977) such as metabolic processes involved in seed germination, requirements for germination of a number of species; some factors affecting germination such as temperature, light, electrical, magnetic and pressure treatments; fungicide, nematocide, herbicide and fertilizer effects; ultra-structural studies and germination equipment.

The effect of presowing, including priming, treatments and pelleting and special sowing techniques on yield is reviewed in the last part of this publication. This section, which includes a review on pelleting for inoculation with nitrogen fixing bacteria, should be of special interest to agriculturalists.

The purpose of this publication is to present a scan rather than a critical discussion of the most recent literature. In this, part 4 has adequately succeeded.

J. G. C. SMALL

METHODS OF STUDYING ROOTING SYSTEMS, by W. Böhm, with pp. xiii + 188 and 69 figures. ISBN 3-540-09329-X. Berlin, Heidelberg, New York: Springer-Verlag, 1979. Volume 33 in the series "Ecological Studies: Analysis and Synthesis", edited by W. D. Billings, F. Golley, O. L. Lange and J. S. Olson. Cloth DM 60, US \$38.00.

This is a very useful book in a valuable series. It meets a much felt want by supplying a systematic handbook on the methodology employed in root studies, and as such it will be welcomed by ecologists and agriculturalists. Its relatively small size might at first give the impression that its coverage cannot be extensive or that its treatment must be superficial in many respects. This is not the case. By careful selection of material and very systematic presentation and illustration of his matter, the author has succeeded in presenting a truly remarkable amount of information. This, of course, is encountered in many such books. But his efforts to evaluate techniques and discuss the relative suitability of methods for various investigations is not so frequently encountered and will be of great assistance to workers new in this field. Also, the forty pages of references will enable workers to proceed further in any specific line than this book does, if they wish to do so.

The book classifies root-study methods into:

- | | |
|-------------------------|-----------------------|
| 1. Excavation methods | 5. Glass wall methods |
| 2. Monolith methods | 6. Indirect methods |
| 3. Auger methods | 7. Other methods |
| 4. Profile wall methods | 8. Container methods |

A special chapter is devoted to the problem of washing techniques in general and the sources of trouble and error involved.

Another separate topic that is treated independently of the methods, is that of the various root parameters in use, how these are determined and what their use is in general root studies.

It is clearly impossible to review all these sections in any detail in such a short review, so I would like to mention some of the things that I found of interest. The section on excavation methods made fascinating reading as it revealed a surprising number of variations of what I had always regarded as a rather tedious technique and it was edifying to note that it was here in South Africa in 1937 that N. G. van Breda introduced the use of compressed air to blow away soil particles from roots: this is the earliest but by no means the last reference to local work in this book, which is also better informed about Mount Edgecomb's Root Laboratory than most local botanists.

The auger sampling section is informative and helpful describing the sort of damage the mechanical augers like the Kelley do to the surrounding soil in causing compaction, etc. Hence the sites on which they can be used are limited. The fact that the auger cores give a reliable rapid root count by the Core Break Method, will interest many readers.

Root profile work is well discussed and new techniques whereby Plexiglass sheets are fixed to the profile are described. Thin transparent foils are mounted on this flat surface and roots, soil profiles and any other data can be mapped on a clean sheet of foil.

Root profiles are important. Hence root laboratories, and later rhizotrons have been designed and built. This book discusses them too. But it comes up with a remarkably simple and cheap device termed a *minirhizotron*, which gives quantitative root data for the first meter of soil. It is a hollow glass or plastic tube with a grid inscribed on it. The

operator uses a mirror and a lamp and sees how many roots have grown in each square. It is possible to map root growth just as accurately as with a root profile in a root laboratory—this seems to be a very useful method indeed.

In the container section, which is also interesting and has many helpful suggestions to make, the one on growing plants in flexible tubes made of polythene or other thin tubing seems very worthwhile, as plants can be grown in large containers when necessary, but the containers take up no space when not in use.

The chapter on root parameters clearly indicates that dry weight is the most important of these and that root length is now increasing in importance, as it can be measured more accurately. For much work the shoot-root ratio still remains important.

This is a good book which will be of great value to the non-specialist wishing to work in this field as well as the specialist wishing to obtain a modern up-to-date view of the whole subject and because of its impeccable historical background, to the teacher.

The main objections to the book are not the authors fault. Dry weight determination of biological matter generally is very unsatisfactory and it is in this book. The ashing procedures recommended to overcome contamination of rooting systems overlook the fact that many roots have appreciable quantities of silica in them. But it is petty to harp about the minor flaws in this book.

K. H. SCHÜTTE



ANNOUNCEMENT

THE 1980 LAWRENCE MEMORIAL AWARD

The Award Committee of the Lawrence Memorial Fund is pleased to announce the selection of Mr James M. Affolter of the University of Michigan as recipient of the 1980 Lawrence Memorial Award. A student of Dr William R. Anderson, Mr Affolter is investigating the taxonomy, evolution and phytogeography of the genus *Lilaeopsis* (Umbelliferae). He will be using the proceeds of the Award in travel to Australia and Tasmania for field studies.

The Lawrence Memorial Fund has been established at the Hunt Institute for Botanical Documentation, Carnegie-Mellon University to commemorate the life and achievements of Dr George H. M. Lawrence, founding Director of the Institute. Proceeds from the Fund are used to make annual awards of \$1,000 to outstanding doctoral candidates for travel in support of dissertation research in any of Dr Lawrence's fields of special interest: systematic botany or horticulture, or the history of the plant sciences, including bibliography and exploration. The Fund has been constituted initially by contributions from the Lawrence family and The Hunt Foundation, augmented by donations from many of Dr Lawrence's friends and colleagues. Additional contributions are welcomed.

SHORT NOTE

**STUDIES IN ORCHIDACEAE FROM SOUTH CENTRAL AFRICA:
CORRECTIONS**

G. WILLIAMSON

It has been found that certain names published in a previous article (Williamson, 1980) are later homonyms. The following corrections are therefore proposed:

Habenaria (sect. *Pentaceras*) **debiliflora** Williamson, nom. nov.

H. debilis Williamson in Jl S. Afr. Bot. **46** (4): 329, fig. I (1980) nom. illegit., non Hook. fil. (1864).

Bulbophyllum infracarinatum Williamson, nom. nov.

B. carinatum Williamson in Jl S. Afr. Bot. **46** (4): 333, fig. 4 (1980), nom. illegit., non Cogn. (1895).

THE PTERIDOPHYTES OF GOUGH ISLAND

J. P. ROUX

(Drakensberg Botanic Garden, Harrismith)

ABSTRACT

The habitats of the twenty-six species of pteridophytes on Gough Island are given.

UITTREKSEL

DIE PTERIDOFIETE VAN GOUGH-EILAND

Die habitatte van die ses-en-twintig varingsoorde wat op Gough-eiland aangetref word, word beskryf.

INTRODUCTION

Gough Island, S 40° 19' 19", W 9° 53' 42", is situated in the mid-south Atlantic ocean and may be regarded as the most outlying island of the Tristan da Cunha group.

This island was first discovered as early as 1505 when it was uninhabited. During the 19th century it was often occupied for short periods and frequently visited when a few, scanty collections of plants were occasionally made. During the mid-20th century the Gough Island Scientific Survey team stayed there from 1955 to 1956.

This was the first survey ever done on the vegetation of Gough Island. Wace (1961), the botanist of the survey team recorded twenty-seven pteridophyte species which was a considerable increase in the number previously known from the island.

Rudmose Brown (1905), mentions ten species of ferns in his paper on the botany of Gough Island and twenty years later, Wilkins (1925), recorded only nine species for the island.

The present author visited Gough Island during the period September to October 1979 in order to study its pteridophytic flora. It was only then that it was realised that three of the species listed by Wace (1961) could not be included in this paper. Wace listed names attached to his collections but these were not checked by a systematist. They were names of any previous Tristan or Gough Island records. The three deleted species are *Lycopodium insulare*, *Elaphoglossum hybridum* and *Polystichum mohroides*.

The present author recorded twenty-six species of pteridophytes for the island.

A list of names which differ from Wace's paper is given below.

Wace	Roux
<i>Gymnogramma cheilanthoides</i>	<i>Eriosorus cheilanthoides</i>
<i>Dryopteris aquilina</i>	<i>Ctenitis aquilina</i>
<i>Dryopteris paleacea</i>	<i>Dryopteris parallelogramma</i>
<i>Thelypteris tomentosa</i>	<i>Amauropelta bergiana</i> var. <i>tristanensis</i>
<i>Asplenium alvaradense</i> (mis-spelled)	<i>Asplenium alvarezense</i>

CLIMATE

The climate of Gough Island has been described as temperate (Wace, 1961). Mean temperatures at the meteorological station at Transvaal Bay between the years 1971 to 1975 at an altitude of 54 m were a maximum of 18,6 °C in February and a minimum of 5,7 °C in July.

An very uneven precipitation pattern occurs on the island. The average rainfall is 3 057 mm per annum. Rain is very frequent with a maximum of 512 mm being recorded in March and a minimum of 80 mm during January for the period from 1971 to 1975. Wace (1961), reported rainfall at an altitude of 600 m from Barren Dome to be 1,5 times as much as that for the same period at Goncalo Alvarez at an altitude of ± 20 m.

With such a high rainfall the average humidity is 80 % and constant throughout the year. Mean humidities recorded on the island are: maximum 82 % for the months July to August and a minimum of 77 % in December.

Mist is frequent on the island but more so at altitudes above 740 m. The sky is usually cloudy which reduces the sunshine on the island to a very large extent. Maximum sunshine is in October when an average of 7,1 hours per day can occur. This drops to an average of 1,96 hours per day in June.

Snow is frequent there in the winter months at elevations above 450 m. However temperatures never drop to freezing point at lower altitudes.

The prevailing wind is westerly and can often reach gale force.

VEGETATION

The age of Gough Island in relation to its vegetation is discussed by Hafsten (1960). Since its discovery in 1505 no signs of any volcanic activity have been reported. Bands of volcanic ash which probably originated from the island itself occur in peat at an depth of 1 350 mm on Albatross Plain. These have been dated at 2 345 years (Wace, 1961). Pollen analyses of peats above and below these depths reveal that any volcanic activity had a negligible effect on the island's plant life.

The bottom of the peat profile on Gough Island has been dated at 4 720

years. There is thus no definite evidence from the peat deposits of any vegetation more than 5 000 years of age.

The conclusion is that the intermittent volcanic activity that did take place during the last few thousand years had little effect on the island's vegetation which at present varies from sub-Arctic to cool temperate in character.

Wace (1961), illustrated that the degree of exposure, as well as altitude are the prime factors which are correlated with the distribution of the present formation. Rock formations are important in influencing the vegetation mainly as in weathering, they have given rise to differing topographies.

In general, the formation with structural similarities to sub-Arctic vegetation is concentrated on the windward or western side of the island. Those of temperate affinities are mainly on the leeward or eastern side, or in sheltered situations.

Five distinct types of vegetation are recognized (Wace, 1961). Each of these formations comprises several different communities. The five major vegetation types can be described as follow: (Fig. 1).

Tussock Grassland

This vegetation type consists of communities of large grasses such as *Poa flabellata* and *Spartina arundinaceae* which form stout tussocks up to 2 m tall which cover most of the cliffs and off-lying sea-stacks.

Fern Bush

Fern bush is very dense and consists of thickets of *Phylica arborea* interspersed with *Histiopteris incisa* and *Blechnum palmiforme* heath. It occurs below 300 m in the south and east as well as in a few sheltered glens to the north. The *Phylica*, *Blechnum* and *Histiopteris* communities are collectively termed fern bush.

Wet Heath

Stunted *Blechnum palmiforme*, *Empetrum rubrum* and various grasses are dominant in this vegetation type which lies between 300 and 600 m above sea level and forms the intermediate zone bordering on all the other vegetation formations on the island, containing thus elements of them all.

Moorland, verging to Feldmark and Montane Rock

Wet heath vegetation can develop up to the highest points on Gough Island in parts where there is protection from prevailing winds. This usually enables peat to accumulate. The area above 600 m is mostly exposed and windswept and bears a montane moorland vegetation on thin mineral soils. In places it verges to feldmark and bare rock.

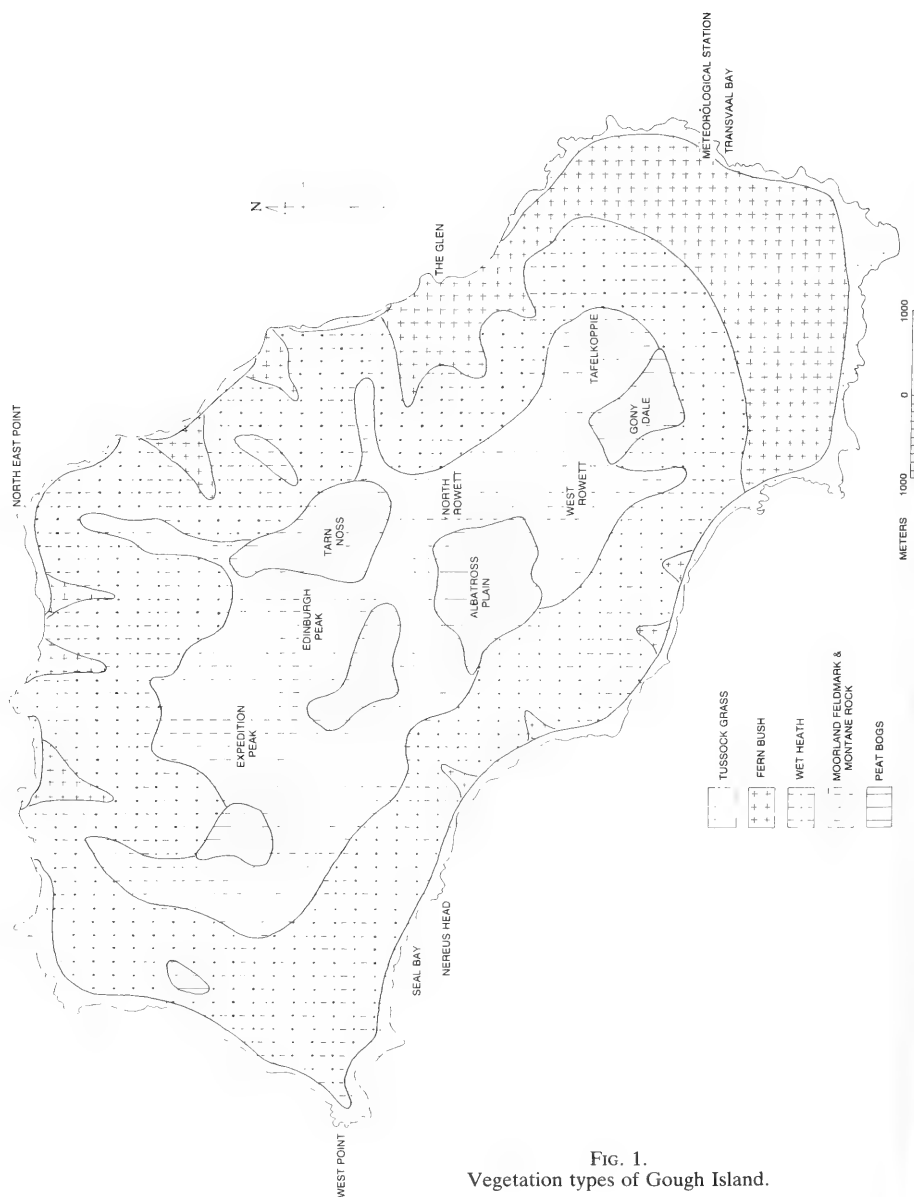


FIG. 1.
Vegetation types of Gough Island.

Peat Bogs

Two different types of bogs bearing two different types of vegetation are found on the upland areas where both valleys and plateaus have impeded drainage.

PTERIDOPHYTE DISTRIBUTION ON GOUGH ISLAND

There is an very uneven distribution pattern of pteridophytic taxa which can be ascribed to the topography as well as to the climatic conditions (Fig. 2).

Sub-Arctic as well as temperate vegetation occurs on the island as the topography is such that typical sub-Arctic conditions are created by the prevailing westerly wind. Cosmopolitan south-Arctic species such as *Lycopodium saururus*, *L. magellanicum*, *Ophioglossum opacum*, *Hymenophyllum peltatum*, *Grammitis billardieri* and *Blechnum penna-marina* are common in these sub-Arctic conditions.

The temperate species are mainly confined to the lower southern and eastern parts of the island which are protected from the westerly wind. Species such as *Hymenophyllum aeruginosum*, *Histiopteris incisa*, *Hypolepis rugulosa*, *Rumohra adiantiformis*, *Asplenium lunulatum*, *A. polyodon*, *A. insulare* and *Blechnum punctulatum* are found in these areas.

Many of these species which originate from the temperate parts of South

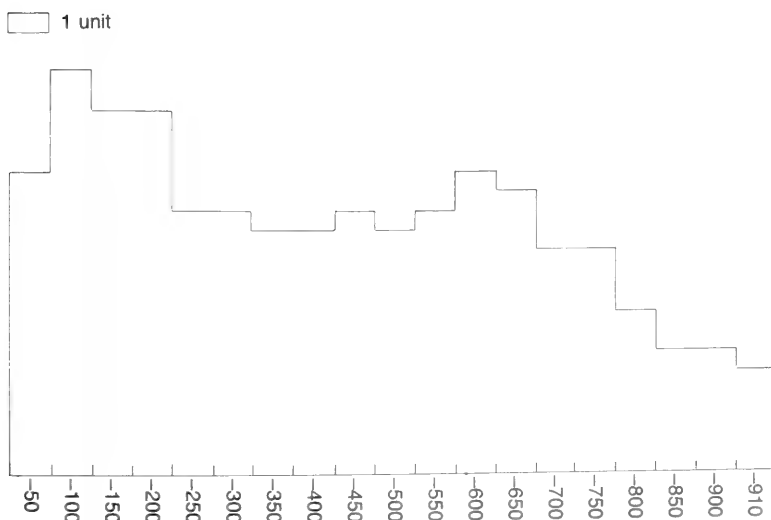


FIG. 2.

Dendrogram showing distribution of pteridophytes on Gough Island.

America have adapted to withstand conditions on the western parts of the island. These plants are usually stunted or grow in protected crevices. Such species are *Hymenophyllum peltatum*, *H. aeruginosum*, *Ctenitis aquilina*, *Elaphoglossum laurifolium*, *E. succisifolium* and *Eriosorus cheilanthoides*.

To summarise, only 29 % of the pteridophytes occur at all altitudes and are fairly evenly distributed over the entire island. 19 % of the taxa are mainly confined to the exposed sub-Arctic conditions with the remaining 52 % confined to the temperate conditions. A reduction in the number of taxa is experienced as the altitude increases (Fig. 2). This can be ascribed to the exposure of the upper parts as well as an increase in rain and a reduction in temperature.

There are twenty-six pteridophyte species recorded on the island and these belong to eleven families which are all cosmopolitan.

A single species, *Asplenium alvarezense* Rud.Br. is endemic to Gough Island.

LYCOPODIACEAE

***Lycopodium saururus* Lam.**, Encycl. Méth., Bot. 3: 653 (1789).

Terrestrial or lithophytic. Plants are large and many-stemmed when growing on protected slopes and among other vegetation on the higher southern and eastern slopes. Depauperate forms are common in bogs and on windswept ridges. Common at altitudes above 600 m. *Roux 743, 751* (NBG).

***Lycopodium diaphanum* Sw.**, Syn. Fil.: 179 (1806).

Plants were recorded at most conditions on the island. It is more common as a pioneer where peat slides have occurred. Seldom found in shaded conditions. Widely distributed on the island between altitudes from 100 to 550 m. *Roux 725, 758* (NBG, K).

***Lycopodium magellanicum* Sw.**, Syn. Fil.: 180 (1806).

Terrestrial or lithophytic. Depauperate forms are common on exposed windswept ridges. Larger plants are confined to taller vegetation and protected conditions. Common on higher (600–900 m) altitudes of the island. *Roux 752, 761* (NBG).

OPHIOGLOSSACEAE

***Opheoglossum opacum* R. Br.**, Prodr. fl. Nov. Holl.: 164 (1810).

This species is deciduous. Active growth starts in October. Growing conditions vary from waterlogged bogs to slightly drier slopes. Common at all altitudes between 550 and 750 m on the exposed western parts of the island. *Roux 770, 771* (NBG).

HYMENOPHYLLACEAE

Hymenophyllum aeruginosum (Poir.) Carm. in Trans. Linn. Soc. 12: 518 (1818).

Trichomanes aruginosum Poir. in Lam., Encycl. Méth. Bot. 8: 76 (1808).

Litho—or epiphytic. This species is common in the south and east areas of the island where it grows in deep shade. Common as an epiphyte on the stems of *Blechnum palmiforme*. Confined to rock crevices at higher altitudes and on exposed western areas. Fairly common all over the island at altitudes between 50 and 950 m. Roux 717 (NBG, K), 742 (NBG).

Hymenophyllum peltatum (Poir). Desv., Prod. 333 (1827).

Trichomanes peltatum Poir. in Lam., Encycl. Méth. Bot. 8: 76 (1808).

Litho—or epiphytic. Common as an epiphyte to the south and east of the island on the stems of *Blechnum palmiforme*. Confined to rock crevices and also slight protection in the west where depauperate forms of this species are quite frequent. Common at all altitudes and aspects of the island. Roux 720, 741, 765 (NBG).

DENNSTAEDTIACEAE

Histiopteris incisa (Thunb.) J. Sm. in Hist. Fil. 295 (1875).

Pteris incisa Thunb. in Prodr. Pl. Cap. 171 (1800).

This is the most common fern species on the southern and eastern parts of the island. The species is deciduous but fronds may reach a length of 1 m. On the lower south-eastern slopes the plants form the dominant vegetation. Mainly confined to the southern and eastern areas of the island at an altitude of 650 m. Very occasionally found in swallow holes above this height.

"*Histiopteris incisa* occurs sporadically in most of the more sheltered communities up to 600 m above sea level. In the glens and on the Southern slopes it dominates extensive areas, often with few associates. At 15 m above the sea near Goncalo Alvarez, loosely packed and moist peat up to 1 m deep is covered by a dense layer of *Histiopteris* with the fronds as much as 90 cm long." (Wace, 1961: 344). Wace (1961: 345) later states, ". . . in open *Phyllica* bush, *Histiopteris incisa* and *Dryopteris aquilina* often form a dense layer beneath the trees up to 1 m in height." Roux 733 (NBG, K, BOL).

Hypolepis rugulosa (Lab.) J. Sm. in Bot. Mag. 72 Comp. 8 (1846).

Polypodium rugulosum Lab., Nov. Holl. pl. spec. 2 (1806).

A terrestrial species confined to streambanks where it is often found growing in shaded conditions. Plants at lower altitudes near the coast are regularly sprayed by waves during heavy seas. A species fairly common on the lower (50–500 m) southern and eastern parts of the island. Roux 723 (NBG), 745 (NBG, K, BOL).

VITTARIACEAE

Vittaria vittarioides (Thouars) C. Chr., Ind. Fil. 655 (1907).

Pteris vittarioides Thouars, Fl. Trist. d'Ac. 31, t. I (1804).

Litho—or epiphytic. A species more frequent on well-protected shaded stream-banks. Depauperate forms are found as epiphytes on the stems of *Blechnum palmiforme*. Confined to altitudes below 150 m to the south and east of the island. Roux 722 (NBG, K).

ADIANTACEAE

Adiantum poiretii Wikstr. in Vet. Akad. Handl. 443 (1825).

The plants are usually confined to sheltered positions on the lower (50–200 m) southern and eastern slopes where they grow as individuals but often in large masses. Common on the southern sea-facing cliffs near the meteorological station. Roux 748 (NBG, K, BOL), 754 (NBG)

Eriosorus cheilanthoides (Sw.) A. F. Tryon in Brit. Fern Gaz. 9: 271 (1966).

Grammitis cheilanthoides Sw., Syn. Fil. 23: 219 (1806).

Terrestrial. A plant adapted to the higher parts of the island. Usually found in moss among rocks which provide some protection. Fairly common between 450 and 750 m. At 450 m the plants are much bigger than those at higher altitudes. Confined to the higher parts of the island. Frequent on the Rowetts. Not observed on the northern parts of the island. Roux 729 (NBG).

GRAMMITIDACEAE

Grammitis billardieri Willd., Sp. Pl. ed. 4, 5: 19 (1810).

A lithophytic plant mainly confined to the higher parts of the island. Common in rock crevices sheltered from the prevailing westerly winds. Depauperate forms are frequent on exposed rock-faces. This species is relatively common at altitudes above 600 m but may be found at lower levels on the western parts of the island. It does not occur on the eastern parts. Roux 744, 763, 764 (NBG).

ASPLENIACEAE

Asplenium alvarezense Rud. Br. in J. Linn. Soc. Bot. 37: 247 (1905).

Endemic to Gough Island. Terrestrial to epiphytic. Usually found in shade on all aspects and in all conditions on the island. Common as an epiphyte on the stems of *Blechnum palmiforme*. Confined to rock crevices and other sheltered positions on the western parts and at higher altitudes. More common in the south and east.

Wace, (1961: 342) says, “. . . and *A. alvarezense* on the sides of the tussock stools are often the only associated species.” This he observed in penguin

rookeries. He later says, (1961: 344), “. . . 15 m above sea near Goncalo Alvarez . . . *A. alvarezense* are abundant on dead *Phylica* logs, . . .”, “Where the surface is very uneven, and where more light reaches the ground, *A. alvarezense* dominates the ground layer . . .” *Roux* 715 (NBG), 769 (NBG, K).

Asplenium insulare Carm. in Tr. Linn. Soc. 12: 512 (1818).

A species observed on the lower eastern slopes of the island. Fairly common but easily overlooked. Usually in exposed conditions among *Histiopteris incisa* but on a few occasions plants were found on streambanks in light shade. Confined to the lower (50–100 m) southern parts of the island. *Roux* 737 (NBG, K).

Asplenium lunulatum Sw. in Schrad., Journ. Bot. 1800, 2: 52 (1801).

Terrestrial. Confined to deep shade and well-sheltered positions which are constantly moist. Observed at two localities on the island. The first, 30 m above sea-level at the waterfall west of the meteorological station and the other 20 m above sea-level in the Glen. *Roux* 749 (NBG, K), 768 (NBG).

Asplenium polyodon Forst. f., Prodr. 80 (1786).

Terrestrial. Not a very common plant and easily overlooked. Usually found in full sun among *Histiopteris* and *Asplenium obtusatum*. Confined to the lower (50–100 m) southern aspects of the island. *Roux* 730 (NBG, K).

Asplenium obtusatum Forst. f., Prodr. 80 (1786).

Terrestrial. Plants can obviously withstand severe conditions as they were located near sea-level where they are regularly within the spray-zone of the sea. Plants are also found in the open and in the shade of *Phylica arborea* but rarely under the canopy of these trees. Common in the south and east of the island up to an altitude of 200 m.

Wace, (1961: 342), made the following observation in a penguin rookery. “. . . and *Scirpus sulcatus* overlying the rocks, and *A. alvarezense* and *A. obtusatum* on the sides of the tussock stools are often the only associated species.” He also says “On the very broken slopes below 300 m in the South-east of the island, *Histiopteris* is partially replaced in the fern bush by *Asplenium obtusatum* and . . . this species can withstand considerable exposure to salt spray, and . . .” (Wace, 1961: 344). *Roux* 728, 732 (NBG), 753 (NBG, K).

THELYPTERIDACEAE

Amauropelta bergiana (Schlechtend.) Holtt. var. *tristanensis* Holtt. in JI S. Afr. Bot. 40 (2): 134 (1974).

Terrestrial. Fairly common along streambanks in very moist and shady conditions. Exposed plants usually smaller. Confined to the lower southern parts of the island below an altitude of 300 m. *Roux* 714, 746 (NBG).

LOMARIOPSIDACEAE

Elaphoglossum laurifolium (Thouars) Moore in Ind. 14 (1857).

Acrostichum laurifolium Thouars, Fl. Trist. d'Ac. 31 (1804).

Terrestrial, litho- or epiphytic. A very variable species in size due to the climatic conditions on the island. Depauperate forms are common on the higher and western parts. Widespread over the entire island. Common in the southern and eastern parts. Not recorded at an elevation above 640 m.

Wace, (1961: 344) says, ". . . *Elaphoglossum laurifolium* is abundant on dead *Phylica* logs, . . ." This observation was made at Goncalo Alvarez. Roux 718, 738 (NBG), 724 (NBG, K).

Elaphoglossum succisifolium (Thouars) Moore in Ind. 15 (1857).

Acrostichum succisifolium Thouars, Fl. Trist. d'Ac. 31 (1804).

Terrestrial, litho- or epiphytic. A species very variable in size. Common in the south and east where it is found in exposed conditions and along streambanks in deep shade. Exposed plants are usually depauperate and generally confined to the western parts of the island. Widespread on the island below an altitude of 650 m. Roux 719 (NBG, K), 727, 750, 766 (NBG).

ASPIDIACEAE

Ctenitis aquilina (Thouars) Pic. Ser. in Webbia 28: 468 (1973).

Polypodium aquilinum Thouars, Fl. Trist. d'Ac. 32 (1804).

Dryopteris aquilina (Thouars) C. Chr. in Ind. Fil. 252 (1905).

Terrestrial. This is one of the few plants which thrive in the relatively deep shade of *Phylica arborea*. Plants are common on streambanks but are more irregularly spread in exposed conditions where they are usually very stunted and only a few fronds are produced. At high altitudes often only a single frond protrudes from the dense formation of grass and mosses. This species is more common on the southern and eastern parts but is frequently found on the upper and western parts of the island. Here the plants are more confined to rock crevices. No plants were observed above 800 m.

Wace, (1961: 345) says, ". . . and *Dryopteris aquilina* often form a dense layer beneath the trees up to 1 m in height." Roux 716, 735 (NBG, K, BOL).

Dryopteris parallelogramma (Kunze) Alston in Amer. Fern Journ. 47: 92 (1957).

Aspidium parallelogrammum Kunze in Linn. 13: 146 (1839).

Terrestrial. A fern species common in the east of the island where it is usually found in very wet conditions on streambanks. Plants were observed in exposed as well as in shaded conditions and no remarkable variation was noted.

The plants usually grow in small groups and develop an erect caudex of up to 200 mm high and 80 mm in diam. Mainly confined to the eastern parts of the island but a single plant was observed at an altitude of 410 m on the southern slopes of Tafelkoppie. In the eastern parts no plants were observed above an altitude of 300 m. *Roux 740* (NBG), *767* (NBG, K, BOL).

Rumohra adiantiformis (G. Forst.) Ching in *Sinensia* 5: 70 (1934).

Polypodium adiantiforme G. Forst., *Prod.* 82 (1786).

Aspidium capense Willd. *Sp. Pl. ed. 4, 5*: 267 (1810).

Terrestrial. These plants form dense stands on the exposed lower southern and eastern parts of the island, resulting in fronds that are relatively smaller and scorched. Active growth takes place during October. Frequent at coastal areas in the south and east. Scarce on the higher parts but frequent along the Albatross Plain margin. Not observed above 660 m.

"On the very broken slopes below 300 m in the South-east of the island *Histiopteris* is partially replaced in the fern bush by . . . and *Rumohra adiantiformis* . . . this species can withstand considerable exposure to salt spray . . ." (Wace, 1961:344). *Roux 739* (NGB, K, BOL).

BLECHNACEAE

Blechnum palmiforme (Thouars) C. Chr. in *Christoph. Results Norw. Sc. Exp. Trist. d'Ac.* 6: 10 (1940).

Pteris palmiformis Thouars, *Fl. Trist. d'Ac.* 30 (1804).

Terrestrial. Common and well developed on the lower southern and eastern parts and widespread over the rest of the island. Plants reduce in size as altitude increases. Stems of up to 1.25 m high were measured on the lower (below 500 m) elevation but the plants are small and usually confined to sheltered positions at the higher altitudes. Numerous new fronds are produced simultaneously during October on the lower parts. No sign of any growth was visible on the upper parts.

Wace, (1961: 344) says, "In the fern bush it dominates extensive areas of ground, often with no associated species except fern epiphytes. The trunks of the *Blechnum* lie in a confused tangle, with their procumbent lower parts buried in the peat, and the upper parts, which are invariably covered in a thick layer of epiphytic ferns, producing a crown of stiff fronds up to 1 m in diameter and often over 1.5 m above ground." He also observed that "Neither *Blechnum palmiforme* nor *Histiopteris incisa* grow in places exposed to much salt spray. . . ." (Wace, 1961: 350). *Roux 736* (NBG, K, BOL).

Blechnum penna-marina (Poir.) Kuhn, Fil. Afr. 92 (1868).

Polypodium penna marina Poir. in Lam., Encycl. Méth. 5: 520 (1804).

Terrestrial, litho- or epiphytic. A very adaptable species. In the south and east the plants are confined to sheltered conditions along streambanks and cliffs. On the upper, more exposed parts plants are more common but very depauperate. This species was observed at all altitudes. Common and widespread over the entire island.

"At 330 m above sea level . . . *Blechnum penna marina* also grow as an epiphyte, . . . on the trunks of the tree-ferns." (Wace, 1961: 351). *Roux* 726 (NBG), 755 (NBG, K), 721 (K).

Blechnum punctulatum Sw. in Schrad., Journ. Bot. 1800, 2: 74 (1800).

Terrestrial or lithophytic. Plants grow in small groups in continual shade of cliffs or of *Phylica arborea*. At Transvaal Bay the plants are also regularly sprayed by the sea. Very localized in the south and east below an altitude of 200 m. *Roux* 731, 747 (NBG, K), 757 (NBG, K, BOL).

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LITTERFALL OF THE EXOTIC ACACIAS IN THE SOUTH WESTERN CAPE

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ABSTRACT

The annual litterfall of four species of Australian acacias naturalised in the Cape comprises 60 % foliage and 30 % reproductive structures and averages 704 g/m² (dry mass). While litter production of this magnitude is typical of subtropical Eucalypt forests, it is more than double the value recorded in evergreen scrub communities in winter rainfall regions. The ground beneath acacia thickets is covered by a layer of litter which has a dry mass per unit area equal to three times that of the annual litterfall, and which, according to the literature, is rich in phosphorous and has a low C/N ratio. Plants adapted to low nutrient levels do not compete successfully on fertilised soils (Specht, 1963), and it is suggested here that, by enriching the soil, acacias make the environment less suitable for indigenous Fynbos plants.

UITTREKSEL

PLANTE-AFVAL VAN UITHEEMSE ACACIAS IN DIE SUID-WESTELIKE KAAP

Die jaarlikse plante-afval van vier Australiese *Acacia*-soorte wat in die Wes-Kaap genaturaliseer het bestaan uit 60 % blaar- en 30 % voortplantingsstruktuur-reste met 'n gemiddeld van 704 g/m² (droë massa). Hierdie plante-afval produksie is tipies van subtropiese *Eucalyptus*-bosse maar meer as twee keer die waarde aangeteken vir immergroen struikgemeenskappe in winterreënvalstreke. Die grond onder *Acacia*-bosse is bedek met 'n laag plante-afval wat 'n droë massa per eenheid area het wat drie keer dié van die jaarlikse plante-afval is, en wat, volgens die literatuur, ryk is aan fosfor en met 'n lae C/N verhouding. Plante wat aangepas is vir 'n lae voedingsvlak kompeteer nie suksesvol op bemeste grond nie (Specht, 1963), en dit word voorgestel dat deur die grond te verryk, die acacias die omgewing minder geskik maak vir inheemse fynbos.

INTRODUCTION

A number of species of exotic Australian acacias are replacing the Fynbos and coastal shrub communities of the south western Cape, South Africa (Hall, 1979). The indigenous vegetation is dominated by small-leaved, sclerophyll, evergreen shrubs, and in structure resembles heathland and some shrubland in regions with mediterranean-type climates (Beadle, 1966; Loveless, 1962; Specht, 1963). The low productivity of the indigenous vegetation is indicated by its low biomass (Kruger, 1977), long lived leaves (Kruger, 1979) and the paucity of plant litter on the ground (Kruger, 1977). The exotic acacias are taller and faster

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growing and produce more litter than most indigenous plants and within a few years have overtopped the natural vegetation, and have covered the ground with a thick carpet of phyllodes, pods and twigs.

The aim of this paper is to compare the litter production and accumulation rate of exotic acacia thickets with that of sclerophyllous vegetation types similar to Fynbos. Hypotheses relating to the differences in productivity and nutrient turn-over of exotic and indigenous vegetation, which arise from this comparison, can be tested when the litterfall studies at present being carried out as part of the Fynbos Biome research programme (Anon., 1978) have been completed.

METHODS

All the data used in this paper were collected in mature, self-established thickets of exotic acacias on the Cape Peninsula and the adjacent Cape Flats between March, 1977 and November, 1978. They provide a quantitative assessment of the masses of the canopy, the annual litterfall and the ground litter.

Canopy mass

Nine *Acacia cyclops* Cunn. ex G. Don. and seven *A. saligna* (Labill.) Wendl. trees of various stem diameters were measured, felled, divided into foliage, twigs and branches exceeding 20 mm in diameter, and then weighed in the field. Each of the components was subsampled, and the dry/wet weight ratio of the sub-sample was used to estimate the dry weight of the entire tree. The mass of the canopy per unit area (i.e. excluding wood and branches over 20 mm in diameter) was calculated from equation (1).

$$\text{canopy mass (g/m}^2\text{) per unit area} = \frac{\text{canopy mass of tree (g)}}{\text{canopy area of tree (m}^2\text{)}} \dots\dots (1)$$

Canopy cover was assumed to be continuous. Total biomass per hectare was the product of total tree mass and tree density per unit area.

Annual litterfall

Ten terylene mesh bags attached to wire hoops 0.5 m diameter and mounted on iron fence droppers were arranged at random in thickets of each of the following acacia species, to catch falling litter: *A. cyclops*, *A. longifolia* (Andr.) Willd., *A. melanoxylon* R.Br. and *A. saligna*. Litter was collected at monthly intervals between May, 1977 and April, 1978, dried at 90 °C for 24 hours and weighed. The standard error on the mean monthly weight of the litter of each species never exceeded 10 %, so that the sum of the monthly means is considered to be a good estimate of the litter production of selected acacia thickets over the 12 month study period.

Ground litter layer

Ground litter was sampled during the winter of 1978. All litter within ten random 1/16 m² quadrats in each thicket was collected, dried and weighed. Although the distribution of the litter was sometimes patchy due to molehills and depressions on the ground, the mean for each study site is used as an estimate of the dry weight of the litter layer at steady state for a particular species.

Decomposition rate

This was not studied in the field, but was calculated from the litterfall and litter layer data, using Olson's (1963) equation (2).

$$K = L/X_{ss} \dots\dots\dots (2)$$

where L = annual litterfall (g/m²); X_{ss} is the litter on the ground at steady state, inclusive of the current year's litterfall (g/m²); and K is the decomposition constant.

The time taken for 95 % of the steady state litter to accumulate or to decay was estimated with the use of equation 3 (Olson, 1963).

$$3/K = T_{95} \% \dots\dots\dots (3)$$

where K is the decomposition constant, and $T_{95} \%$ decay or accumulation time.

RESULTS

Biomass of acacia thickets in the south western Cape (Table 1) is about ten times greater than that of mature Fynbos (11–26 t/ha dry mass: Kruger, 1977; Kathan, unpubl. data) and shrublands in other regions with mediterranean type climates (15–30 t/ha dry mass: Mooney, 1977). Like other evergreen shrubs (Mooney, 1977; Chapman, 1967), acacias lose about 10 % of their standing crop annually as litter, most of which is derived from the canopy (Table 1), but the actual mass of the litterfall per unit area is 3–4 times greater in acacia thickets than in low heath and shrub communities in mediterranean regions, since the acacias have a larger total biomass.

In a mature healthy thicket, very little of the acacia litter is woody. Phyllodes constitute the bulk of the litter (Table 2), while flowers, pods and seed together contribute about 30 % to the total annual dry mass of the litterfall. Twigs and caterpillar fras are variable, minor components. About half of the canopy mass is renewed annually. The litter accumulates on the ground, and in a mature thicket, the dry mass of the ground litter per unit area exceeds that of the living canopy (Table 1).

TABLE 1.

Litterfall and litter layer of *A. cyclops* and *A. saligna* compared with the total biomass and canopy masses of these species in the south west Cape.

	<i>A. cyclops</i>	<i>A. saligna</i>
Biomass (t/ha dry mass)	131 (4) ¹	135 (10) ¹
Litterfall as % of biomass	7,4	6,0
Litter layer as % of canopy mass	21,2	15,5
Canopy mass (t/ha dry mass)	22 (18)	12 (21)
Litterfall as % of biomass	43,5	68,0
Litter layer as % of canopy mass	125,0	177,3

¹: % error on mean is given in parenthesis

TABLE 2.

Components of annual litterfall of exotic acacias in the south-western Cape

Components	<i>A. cyclops</i>	<i>A. longifolia</i>	<i>A. melanoxylon</i>	<i>A. saligna</i>
Total litter (g/m ²)	968	543	503	804
Flowers %	1,4	10,6	6,7	8,7
Pods %	35,5	16,0	0,5	12,1
Seed %	5,3	8,3	0,3	8,0
Twigs %	11,3	2,6	26,5	10,0
Unident. & fras %	7,7	0,8	2,7	10,4
Phyllodes % ...	39,0	61,7	63,3	60,8

The annual litter fall of the four species studied (averaging 704 ± 110 g/m²/p.a.) is comparable with that of forests in the sub-tropical and warm temperate regions of south east Queensland, New South Wales, Victoria and South Australia (400–800 g/m²/p.a.: Rogers & Westman, 1977; Maggs & Pearson, 1977; Attiwill, 1968; Ashton, 1975; Ashton & Frankenberg, 1976). The litterfall of evergreen scrub communities in mediterranean type climatic regions is about 200 g/m²/p.a. (Mooney, 1977; Specht & Rayson, 1957), which falls short of the averages for warm temperate (550 g/m²/p.a.: Bray & Gorham ex Birk, 1979) and even cool temperate regions (300–400 g/m²/p.a.: Kozlowski, 1973). This low productivity has been attributed to the summer drought which limits photosynthesis, and to the poverty of the soils (Mooney, 1977; Specht, 1973). The south western Cape, where high productivity acacias are replacing low productivity heath- and shrubland, without the assistance of artificial fertilisers, provides a natural experiment for the study of differences in the growth and nutritional strategies of these plants.

The ground litter layer of the acacia thicket weighed between 1 400 and 2 800 g/m², which is fairly average by world standards, but greatly exceeds the

99–495 g/m² recorded in mature mountain Fynbos (Kruger, 1977). That there is a marked difference in the accumulation of litter under exotic acacias and indigenous vegetation is clearly seen in the field. Under acacia thickets, the litter layer forms a carpet 20–40 mm deep, unbroken except where disturbed by moles. Under Fynbos and other indigenous communities, the litter is thin and patchy. Litter covers an average of 15 % of the soil surface under Fynbos on Table Mountain, Cape Peninsula ($n = 31$; Glyphis, 1976), 12 % under coastal bush ($n = 50$; S. J. Milton, unpubl.) and 5 % under the dry Fynbos on Piquetberg, south western Cape ($n = 36$; H. P. Linder, unpubl.).

The mass of the annual litterfall of acacias in the south western Cape was equal to about one third of the mass of the ground litter, giving the decomposition constant a value of between 0.326 and 0.384. When litterfall and ground litter dry weights of the exotic acacias are plotted on Olson's (1963) graph (Fig. 1) which shows the relationship between these parameters for a wide range of

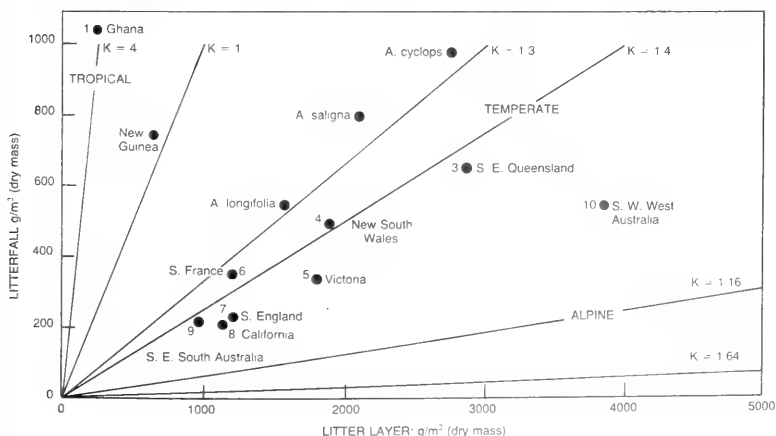


FIG. 1.

Decomposition rates of the litter of exotic acacia thickets in the South western Cape compared with those of other plant communities, world wide. The decomposition rate is represented by the slope of the line (K). The figure is based on that of Olson, (1963), and the points plotted represent K values given in the following papers:

- | | | |
|------|-----------------------------------|----------------------|
| 1, 2 | : Edwards, 1977 | (Tropical forest) |
| 3 | : Rogers & Westman, 1977 | (Eucalypt forest) |
| 4 | : Maggs & Pearson, 1977 | (Coastal scrub) |
| 5 | : Attiwill, 1968 | (Eucalypt forest) |
| 6 | : Lossaint, 1973 | (Dry Quercus forest) |
| 7 | : Chapman, 1967 | (Heath) |
| 8 | : Mooney, 1977 | (Chaparral) |
| 9 | : Lee & Correll, 1978 | (Sclerophyll forest) |
| 10 | : Hatch ex Rogers & Westman, 1977 | (Eucalypt forest) |

plant communities, the slope of the line (K) lies realistically between the lines for tropical regions (which can exceed 1,00) and for temperate regions (about 0,25).

The time taken for 95 % of the steady state litter to accumulate or to decompose was estimated from equation 3. The estimated value of between 7 and 9 years for exotic acacias in the south western Cape is faster than the decomposition rate in temperate and boreal conifer forests or in Chaparral (Olson, 1963; Mooney, 1977). Kruger's (1977) data show that litter under Fynbos may have reached equilibrium within six years: but, even if Fynbos litter were to decay as rapidly as it fell (which is unlikely in a mediterranean-type climate) this would not account for the paucity of the litter layer. As in other mediterranean scrub communities, the lack of litter on the ground under Fynbos must be attributed to very low litterfall values.

DISCUSSION

The nitrogen and phosphorous content of the foliage of Australian acacias (Ashton, 1975; Everist, 1969) exceeds that of sclerophyll vegetation on nutrient poor soils (Lossaint, 1973; Maggs & Pearson, 1977; Lee & Correll, 1978) and is 2-4 times as great as that of Fynbos plants (A. B. Low, unpubl. data). This difference is also reflected in the protein content of acacia shoots ($15,2 \pm 1,0$ %: Everist, 1969) which is about three times as high as that of browseable shrubs sampled in plant communities in the Fynbos Biome: 3,5-6,0 % (Joubert & Stint, 1979). Since the average annual litterfall of the exotic acacias is also three times as great as values cited for mediterranean scrub types (Fig. 1), the annual nitrogen and phosphorous input by acacia litter should be about nine times as great per unit area, as that of Fynbos.

Assuming a nitrogen content of 1,5 % and a phosphorous content of 1,13 %, acacia litter would contribute $10,5 \text{ g/m}^2 \text{ N}$ and $0,92 \text{ g/m}^2 \text{ P}$ to the soil each year, as compared with $1-3 \text{ g/m}^2 \text{ N}$ and $0,03 \text{ g/m}^2 \text{ P}$ in Garrigue, Chaparral and South Australian sclerophyll forest (Loissaint, 1973; Mooney & Parsons, 1973; Lee & Correll, 1978).

The rapid decomposition of acacia litter (7-9 years) as compared to the 13-15 years taken for 95% of the litter of sclerophyll scrub types to decay, might be explained by the fact that the low C/N ratio of acacia litter favours microbial activity (Birk, 1979; Ashton, 1975).

Apart from the nitrogen added to the soil by the litter, the activity of the symbiotic bacteria in acacia nodules fixes nitrogen, changing the soil nitrogen status (Nakos, 1977; Langkamp *et al.*, 1979). The total input of nitrogen to an *A. mearnsii* plantation has been estimated to be in the order of $20 \text{ g/m}^2/\text{p.a.}$ (180 lb/acre/p.a. ; Hallsworth, 1958). Acacias, probably due to the presence of mycorrhiza, are also able to accumulate phosphorous (Barrow, 1977).

There is evidence that the addition of nutrients to oligotrophic, sclerophyll

ecosystems increases their growth rate thereby upsetting the water balance of the plant community and killing species with strong summer growth rhythms (Specht, 1973). This results in the opening up of the sclerophyll community, and an increase in the number of annuals and spring-growing exotic perennials (Specht, 1963, 1973). It follows that Fynbos communities, which also have a summer growth rhythm (J. Sommerville, unpubl.; Kruger, 1979), are found on some of the most nitrogen and phosphorous deficient soils in the world (A. B. Low, unpubl. data) and probably conserve nutrients by storage and internal cycling (Specht, 1963; Kruger, 1979). Such stress-tolerant plants would not be expected to compete successfully on a nutrient enriched soil (Grime, 1977). The prevalence of grasses (indigenous and exotic) on areas recently cleared of acacias may be further evidence for the change in the soil nutrient status which acacias effect.

CONCLUSION

Their evolution in a temperate climate, their early and extended growing season, their tall growth habit and their freedom in the Cape from effective predators and pathogens, have all contributed to the success of the Australian acacias in the Fynbos biome (Milton, 1980). This paper suggests that another important factor in favour of the acacias is their ability to maintain a high rate of litterfall and litter turn-over, and by so doing to boost the nitrogen and phosphorous status of the soil. This nutrient enrichment may be one of the factors enabling the exotic acacias, once introduced to an area, to maintain a hold among indigenous shrubs, and eventually to change, degrade and replace the original Fynbos vegetation.

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**STUDIES IN THE GENERA OF THE DIOSMEAE (RUTACEAE):
10. A REVIEW OF THE GENUS EUCHAETIS**

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ABSTRACT

The twenty-three species belonging to the genus *Euchaetis* Bartl. & Wendl. are listed with diagnoses and keys. Species not recently published are described in detail from fresh material with up-to-date distribution maps and lists of specimens examined. *Euchaetis dubia* Sond. is transferred to *Macrostylis*.

UITREKSEL

**STUDIES IN DIE GENERA VAN DIE DIOSMEAE (RUTACEAE):
10. 'N OORSIG VAN DIE GENUS EUCHAETIS**

Die drie-en-twintig soorte van die geslag *Euchaetis* Bartl. & Wendl. met diagnose en sleutels word gekatalogiseer. Soorte nie onlangs gepubliseer nie word van vars materiaal beskryf. *Euchaetis dubia* Sond. is na die geslag *Macrostylis* oorgedra.

HISTORICAL BACKGROUND

The generic name *Euchaetis*, meaning "beautifully tufted with hairs", was proposed by Bartling & Wendland in their revision of the *Diosmeae* published in 1824. They placed only one species, *E. glomerata* in their new genus but two other species with bearded petals, which they placed in *Acmadenia*, *A. laevigata* and *A. pungens*, have since been transferred to *Euchaetis* as *E. meridionalis* and as *E. pungens*.

Ecklon and Zeyher, in their revision of the *Diosmeae* (1835), recognised four species of *Euchaetis* two of which, *E. elata* and *E. flexilis*, have been upheld. They mistakenly applied the name *E. glomerata* B. & W. to a species from near Caledon, later to be named *E. linearis* by Sonder, and proposed the new name *E. abietina* for a species from near Clanwilliam which had already been named *E. glomerata*.

Sonder in his revision of the *Rutaceae* for the *Flora Capensis* (1860) recognised five species in the genus *Euchaetis*, three of which had been previously published. In addition he proposed the name *E. linearis* for the species found by

Ecklon & Zeyher near Caledon and, doubtfully, the name *E. dubia* for another species, (*Zeyher 291*), from the west coast. The material available to Sonder did not properly show that the style and filaments could elongate considerably, characters which have led to the transfer of this species to the genus of *Macrostylis* in this work. Unfortunately, Sonder was unaware of the work done by Turczaninow who had named the same collection, *Zeyher 291*, *Acmadenia cassioides* in 1858. Turczaninow also saw the flower in its earlier stage before the elongation of the style and filaments and, as it possessed rather large staminodes, he placed it in *Acmadenia*.

Schlechter published two names in 1898, *E. longibracteata* and *Acmadenia diosmoides*, of which the latter has since been transferred to *Euchaetis*. Unfortunately he got his cited specimens switched and this has led to a certain amount of confusion in typification. In 1900, Professor Schinz, who was a great friend of Rudolph Schlechter, named the plant which Schlechter had collected at Sir Lowry's Pass, *E. schlechteri* in honour of his friend.

Dümmer in the *Kew Bulletin* (1912) published four new names, two of which, *E. burchellii* and *E. ericoides*, are upheld while *E. bolusii* and *E. radiata* are now considered to be synonyms of *E. longibracteata* Schltr.

In 1913 Phillips proposed the name *Euchaetis uniflora* for a plant with relatively large pink flowers from near Albertinia. Unfortunately it turned out to be better placed in *Acmadenia* and the new combination, *Acmadenia uniflora* (Phillips) Phillips, was made by Phillips in the *Journal of South African Botany* in 1943.

It is quite certain that our knowledge of this genus would have been very incomplete had it not been for the very active and accurate work on the part of Miss Elsie Esterhuysen whose many collections of these insignificant plants from all parts of the southern Cape Province, are housed in the Bolus Herbarium.

GENERIC DESCRIPTION

Euchaetis Bartl. & Wendl., *Diosmeae* in Beitr. Bot. 1: 15 (1824); A. Juss. in Mém. Mus. Hist. Nat., Paris 13: 472 (1825); Don, Gard. and Bot. 1: 785 (1831); Eckl. & Zeyh., Enum. Plant.: 104 (1835); Endl., Gen. Plant. 2: 1158 (1840); Lindl., Veg. Kingd.: 471 (1853); Sond. in Flor. Cap. 1: 371 (1860); Benth. & Hook., Gen. Plant. 1: 289 (1862–1867); Engl., Pflanzenfam. 19a: 276 (1931); Dyer, Gen. S. Afr. Flow. Pl. 1: 291 (1975). Type species: *E. glomerata* Bartl. & Wendl.

Shrubs 0.3–1.5 m, usually less than 1 m tall, erect, and, with one or two exceptions, single-stemmed at base. *Branchlets* fairly erect, slender, glabrous or puberulous. *Leaves* 2–15 mm long, 0.9–4 mm broad, linear, linear-lanceolate, narrowly lanceolate, lanceolate, broadly lanceolate, elliptic, ovate or orbicular;

flat, round-backed, sub-complicate, or subulate; erect or spreading, alternate or opposite. *Inflorescence* terminal, solitary or twin or aggregated into heads of up to 60 florets, flowering at different times and, except in the case of *E. longibracteata*, without any conspicuous involucreal leaves. *Flowers* subtended by one, or rarely two, bracts and two bracteoles. *Petals* five, distinctly divided into claw and limb; *claw* transversely bearded above, ciliate on the margins and narrowing below, forming a cage around the reproductive parts of the flower; *limb* white or pale pink, usually spreading. *Staminodes* five, rarely absent, usually a vestigial sessile gland, 0,05–0,2 mm long. *Filaments* five, usually about 1 mm long, glabrous, acicular. *Anthers* five, dorsifixed; apical gland globose, minute, usually 0,05–0,2 mm long. *Pollen* 28–55 μ average 46 μ long, 18–35 μ average 25 μ broad, ellipsoid, yellow, sticky, triporate. *Disc* enveloping, obvallate or spreading, exceeds the ovary. *Stigma* 0,2–1,0 mm diam., capitellate or capitate globose. *Style* becoming 0,5–1,6 mm long, glabrous, erect, or, at some stage, deflexed. *Ovary* 5-carpellate, except for *E. tricarpellata*, 0,7–1,0 mm diam.; apices globose, usually glabrous or sparsely setulose, in one case, *E. vallis-simiae*, densely pubescent. *Fruit* 5-carpellate, except for *E. tricarpellata*, glabrous, sparsely setulose or, in the case of *E. vallis-simiae*, puberulous; *horns* 0,5–7,0 mm long, but mostly in the 1 to 2 mm range, in the case of *E. pungens* deeply cleft at the apex. *Seeds* black, shining except in the case of *E. ericoides*, *E. glomerata* and *E. tricarpellata* where matt.

Characters which distinguish the genus *Euchaetis* are: the transversely bearded, ciliate petals which totally screen the gynoecium and androecium (Fig. 1); the very short filaments and style which do not lengthen greatly but which remain within this enclosure; the staminodes being vestigial or absent; the anthers with a very small, usually globose, apical gland and the glabrous style and filaments.

DISTRIBUTION

Plants belonging to the genus *Euchaetis* are to be found growing only in the south and south western Cape within an area defined by the Cape Geological Series as shown by a dotted line in the distribution map (Fig. 2). From the north, near the Pakhuis Pass in the Clanwilliam Division, the area of distribution extends southwards in mountainous regions to near the mouth of the Palmiet River in the Caledon Division. On an approximate east-west axis, starting from the Uilenkraal River near Danger Point, the area of distribution extends eastwards, mostly on the coastal and limestone hills, to Herolds Bay near George. From here there is a discontinuity of 155 km eastwards until two species appear on the Baviaanskloof and Cockscomb mountains.



FIG. 1.

Typical flower of the genus *Euchaetis*, with two petals removed, showing the androecium and gynoecium totally screened by the transversely bearded petals.

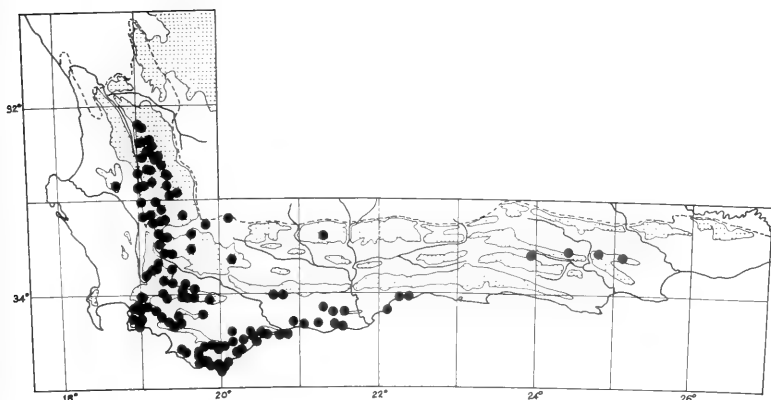


FIG. 2.
Distribution of the genus *Euchaetis*.

KEY TO THE SPECIES OF *EUCHAETIS*

- | | | |
|---------|--|---------------------------|
| 1 | Disc closes over the ovary at first | 2 |
| 1+ | Disc obvallate or spreading as in <i>Diosma</i> | 11 |
| 2 | Fruit tricarpellate | 9. <i>tricarpellata</i> |
| 2+ | Fruit 5-carpellate | 3 |
| 3 | Fruit with horns 0.5 mm long, deeply cleft | 1. <i>pungens</i> |
| 3+ | Fruit with horns not deeply cleft | 4 |
| 4 | Leaves, bracts, bracteoles and sepals gibbous behind the apex | 10. <i>vallis-simiae</i> |
| 4+ | Leaves etc. not gibbous behind the apex | 5 |
| 5 | Leaves opposite, never alternate | 6 |
| 5+ | Leaves opposite or alternate on the same plant | 9 |
| 6 | Leaves with a prominent gland-stepped or scabrous midrib | 5. <i>scabricosta</i> |
| 6+ | Leaves with gland dots scattered in the vicinity of the midrib | 7 |
| 7 | Leaves orbicular | 2. <i>laevigata</i> |
| 7+ | Leaves lanceolate | 8 |
| 8 | Shrub dense, many-stemmed at base of plant | 4. <i>burchellii</i> |
| 8+ | Shrub sparse, single-stemmed at base of plant | 3. <i>albertiniana</i> |
| 9 (5+) | Leaves sparsely pubescent, alternate, sometimes opposite at base | 7. <i>intonsa</i> |
| 9+ | Leaves glabrous, opposite or alternate | 10 |
| 10 | Leaves broadly lanceolate, sub-complicate | 6. <i>meridionalis</i> |
| 10+ | Leaves lanceolate, fairly flat | 8. <i>ericoides</i> |
| 11 (1+) | Disc obvallate, not closing over the ovary and not spreading | 12 |
| 11+ | Disc open, margin sinuate crenulate, exceeds the ovary at first | 19 |
| 12 | Conspicuous involucre leaves present | 17. <i>longibracteata</i> |
| 12+ | Involucre leaves absent | 13 |
| 13 | Style at all stages erect, petals 5.5 mm long | 11. <i>cristagalli</i> |
| 13+ | Style at some stage deflexed, petals 5 mm long or less | 14 |
| 14 | Leaf margins villous-ciliate (not crisped ciliate), petals acute | 12. <i>avisylvana</i> |
| 14+ | Leaf margins not villous-ciliate, petals obtuse | 15 |
| 15 | Leaves obtuse, apex sacculate, margins broadly translucent | 15. <i>flexilis</i> |
| 15+ | Leaves acute or if obtuse, apex not sacculate | 16 |

16	Leaves petiolate, flat, orbicular, 4 mm long	16. glabra
16+	Leaves not flat	17
17	Leaves ovate, obtuse, fleshy, spreading	18. esterhuyseniae
17+	Leaves lanceolate or linear-lanceolate, adpressed	18
18	Fruits with horns 0,5–1,0 mm long, apical flowers opening first	13. elata
18+	Fruits with horns 3,5 mm long, apical flowers last to open	14. glomerata
19 (11+)	Disc open, sinuate-crenulate, style erect at all times, stigma 0,6–1,0 mm diam., capitate	23. schlechteri
19+	Disc open, sinuate-crenulate, style at some stage deflexed, stigma 0,2–0,5 mm diam., capitellate	20
20	Leaves obtuse, apex thickened	19. elsieae
20+	Leaves acute	21
21	Leaf apex incurved mucronate	22. diosmoides
21+	Leaf apex with a straight sharp mucro	22
22	Fruit with horns 1,5 mm long	20. linearis
22+	Fruit with horns 7 mm long	21. longicornis

1. *Euchaetis pungens* (Bartl. & Wendl.) Williams in Jl S. Afr. Bot. **40** (4): 279 (1974).

Acmadenia pungens Bartl. & Wendl., Diosmeae in Beitr. Bot. **1**: 64 (1824). Type: L. hand specimen on sheet No. 4784 in Willdenow's herbarium, received from Jacquin (B, holotype; W, isotypes). *Acmadenia harveyana* Schltr. nom. nud.

The following description, from fresh material, amplifies that given by Bartling and Wendland in 1824.

Shrubs up to 0,7 m tall, rigidly bushy, single-stemmed with a rough warty bark at base, growing in drift sand. *Branches* glabrous, rough, dirty-brown, devoid of leaves, variously bent. *Branchlets* dichotomous, very short, minutely puberulous between the leaves, densely clothed with leaves. *Leaves* 2,8–5 mm long, 2,5–4 mm broad, ovate or elliptic, acute, mucronate, sessile, sub-amplexicaulate, sub-complicate, greyish-green, glabrous, quite thick, opposite, decussate, crowded, erect-spreading; margins thick, cartilagenous, minutely ciliolate; abaxial surface with a few scattered gland dots. *Inflorescence* terminal, sessile, normally twin, without conspicuous involucre leaves. *Bract* one, leaf-like, 3 mm long, 2,3 mm broad, orbicular, acute, mucronate, ciliolate, glabrous, gland-dotted, sub-complicate, sessile. *Bracteoles* two, 3 mm long, 1,6 mm broad, oblanceolate, acute, mucronate, glabrous, 1–2 gland-dotted; midrib quite thick; margins pellucid, ciliate. *Calyx lobes* five, 4 mm long, 2,3 mm wide, elliptic, acute, mucronate, greenish and thickened above, glabrous; margins ciliate, broadly translucent. The lobes are more bract-like than usual being deeply divided. *Petals* five, 5,2 mm long, overall; *limb* 2 mm long, 1 mm broad, oblanceolate, acute, glabrous, recurved, apex with one or two minute hairs; *claw* 3,2 mm long, 1,3 mm broad, with a dense erect bushy transverse beard above, upper part of the translucent margins densely crisped ciliate, midrib fringed with hairs. *Staminodes* five, vestigial, 0,2 mm long, deltoid or completely absent. *Filaments* five, becoming 1,5 mm long, subulate, glabrous. *Anthers* five, before

anthesis 1,3 mm long, 0,8 mm broad, cuneiform-ovoid, orange-yellow; apical gland minute. *Pollen* 50 μ long, 25 μ diam., obloid. *Disc* exceeds and closes over the ovary at first, green, exudes nectar. *Stigma* 0,7 mm diam., globose, green. *Style* becoming 1,3 mm long, erect, glabrous, sub-5-angular. *Ovary* 5-carpellate, 1 mm diam., apices pubescent. *Fruit* 5-carpellate; *carpels* 6–8 mm long, glabrous below, puberulous towards the apex; *horns* divided into two to each carpel, 0,5 mm long, obtuse. *Seed* 5,5 mm long, 2,5 mm broad, black, shining; aril white without any trace of black.

Euchaetis pungens is recognised as distinct with its rigid prickly habit, having the anther cuneiform-ovoid in shape, the disc closing over the ovary with a 5-sided aperture fitting the 5-sided stigma, having evanescent staminodes and having a fruit with the horns deeply divided. It has also been noted that the calyx lobes are unusually deeply divided.

2. *Euchaetis laevigata* Turcz. in Bull. Soc. Imp. Nat. Mosc. **31**: 1: 438 (1858). Type: between Cape Agulhas and Potberg, on limestone hills, under 500 ft., 3/8/1831, *Drège IV, C, a, 2* (BM, E, K, MEL, P, S, isotypes).

Acmadenia laevigata E. Mey. in *Drège Zwei Pflanzen*. Doc.: 122, 161 (1844). nom. nud.

Acmadenia assimilis Sonder in *Flor. Cap.* **1**: 383 (1860). Type: as above.

Euchaetis laevigata differs from both *E. scabricosta* and *E. meridionalis* in having leaves that are always opposite with the midrib recurved, somewhat smaller, orbicular in outline with gland dots scattered and not just on midrib and margins. The shoots are dry without any trace of resin or wax. A detailed description, from fresh material, has been given in the *Journal of South African Botany* **44** (4): 333 (1978).

3. *Euchaetis albertiniana* Williams in *Jl S. Afr. Bot.* **41** (3): 167 (1975). Type: CAPE—3421 (Riversdale): Near Askop on south side of road 16 km west of Albertinia (-AB), 180 m alt., 2/3/1974, *Williams 1879* (NBG, holotype; K, PRE, STE, isotypes).

Euchaetis albertiniana is recognised as distinct from *E. burchellii* Dümmer in that it is destroyed by fires whereas *E. burchellii* develops a stout rootstock from which it may regenerate after fires—a character seldom noted on herbarium sheets. However, the leaves in *E. albertiniana* are often adpressed, ciliolate with an apical callus, whereas those of *E. burchellii* are never so. The anther in *E. albertiniana* possesses a small pointed gland, but that of *E. burchellii* is minute. *E. albertiniana* differs from *E. laevigata* Turcz. which has leaves complicate, orbicular, spreading and somewhat more recurved towards the apex with the apical gland on the anther minute as in *E. burchellii*. *E. albertiniana* is found in the vicinity of Albertinia. *E. burchellii* is more widespread being found in sandy soil from beyond Great Brak River in the east to Uilenkraal River near Gansbaai in the west.

4. *Euchaetis burchellii* Dümmer in Kew Bull.: 90 (1912).

Type: CAPE—3422 (Mossel Bay): sandy hills near the landing place, Mossel Bay (on shrubby sandy dry hills close to our station near landing place Mossel Bay), 18/10/1814, *Burchell* 6239 (K, holotype).

Shrubs to 1 m tall forming a dense bush with many stems arising from a stout rootstock. *Branches* short, fairly erect, bark scaly and rough. *Branchlets* numerous, slender, very short, puberulous, well-clothed with leaves. *Leaves* to 4,5 mm long, 1,5 mm broad, lanceolate, obtuse without any mucro, sub-trigonal, glabrous, eciliate, sessile, opposite, erect, sub-imbricate, decussate, about twice times longer than the internodes. *Inflorescence* terminal, usually twin, white or pink. *Bract* one to each flower, 1,9 mm long, 1,3 mm broad, ovate, obtuse, glabrous, thickened towards the apex, sessile, very sparsely ciliate, midrib 1–2 gland-dotted. *Bracteoles* two, 1,6 mm long, 0,8 mm broad, elliptic, obtuse, glabrous, apex thickened; margins broadly translucent, ciliolate. *Calyx lobes* five, 2 mm long, 1,5–2 mm broad, roughly orbicular, glabrous; apex blunt, trigonal, green; margins broadly translucent, ciliolate. *Petals* 3,7–4 mm long, 2,5 mm broad; *limb* orbicular, 1–2 gland-dotted; *claw* transversely bearded, midrib pubescent, margins ciliate. *Staminodes* vestigial, 0,15 mm long, 0,1 mm diam. *Filaments* five, 1,3 mm long, pale, acicular. *Anthers* five, 0,6 mm long, wine-coloured; apical gland minute. *Pollen* 52 μ long, 32 μ broad, ellipsoid with three longitudinal grooves. *Disc* closes over the ovary at first. *Stigma* 0,5 mm diam., globose, capitate. *Style* becoming 1,5 mm long, erect, persisting. *Ovary* 5-carpellate, 0,7 mm diam., with a few hairs at the sides towards the apex of each segment. *Fruit* 5-carpellate, 6 mm long overall, glabrous, gland-dotted; *horns* 1,2 mm long, clasping a gland at the tip. *Seed* 4,2–4,8 mm long, 1,8–2 mm broad, black, shining; aril white.

Euchaetis burchellii is a lowland coastal species found growing in stabilised wind-blown sand never very far from the sea, at altitudes of from 33 to 250 metres above sea level. Its geographical range extends from Herolds Bay near George in the east to the Uilenkraals River near Gansbaai in the west, a distance of about 275 km.

It is a dense shrub with many stems arising from a stout rootstock, having leaves lanceolate, obtuse, eciliate, without any apical callus and never adpressed.

It is perhaps closest to *E. albertiniana* Williams which however is a fairly diffuse shrub, single-stemmed at base with leaves sometimes adpressed and with a small apical callus. It differs from *E. laevigata* Turcz. which has leaves sub-complicate, orbicular and spreading and is found growing upon limestone to the east of Bredasdorp.

SPECIMENS EXAMINED

CAPE—3419 (Caledon): Witkoppies near Awila, Bredasdorp Division

(-DA), 100 ft., 2/8/1973, *Williams 1834* (NBG); Awila near Strandskloof, Bredasdorp Division, 175 ft., 29/8/1971, *Williams 1518* (NBG), 150 ft., 9/9/1976, *Williams 2203* (NBG); limestone hills near Gansbaai, Bredasdorp Division, -/1/1948, *Lewis 3097* (SAM); Baardscheedersbosch, Bredasdorp Division, 25/1/1948, *Barker 5308* (BOL); Hagelkraal River, Bredasdorp Division, 27/12/1946, *Leighton 2544* (BOL); Groothagelkraal, Bredasdorp Division, 200/400 ft., 24/4/1978, *Williams 2488* (NBG), 400 ft., 28/4/1975, *Oliver 5893* (STE); Elim/Uintjieskuil, Bredasdorp Division, 600 ft., 30/1/1973, *Williams 1754* (NBG); Elim, Bredasdorp Division (-DB), 400 ft., 18/4/1896, *Schlechter 7620* (BM, G, GRA, K, P), 500 ft., 22/4/1896, *Schlechter 7684* (BOL, PRE), 21/6/1972, *Williams 1655* (NBG); Klein Blomfontein, Bredasdorp Division, 300 ft., 15/1/1968, *Van Breda & Admiraal 2303* (K); south slopes Bredasdorp Mountains, Boskloof, 800 ft., 16/11/1972, *Williams 1734* (NBG); Rietfontein Poort, Bredasdorp Division, 150 ft., 11/1/1972, *Williams 1625* (NBG); Soetanyberg above Suur en Soet, Bredasdorp Division, 350 ft., 29/3/1971, *Oliver 3362* (STE); Soetanyberg above Hangnes, 600 ft., 25/5/1978, *Williams 2506* (NBG); sandy slopes at foot of low mountain at Brandfontein, Bredasdorp Division (-DD), 13/10/1951, *Esterhuysen 19016* (BOL, K, LD, NBG).

— 3420 (Bredasdorp): in collibus prope Bredasdorp (-CA), 300 ft., -/7/1895, *H. Bolus 8477* (BOL), *8471* (K); Nachtwacht near Jantjiesbosch, Bredasdorp Division, 150 ft., -/6/1927, *Smith 4290* (K); Voelklip/Graslaagte, Heidelberg Division (-BD), 200 ft., 27/10/1972, *Williams 1715* (NBG); Rondekop above Melkhoutkraal, 600 ft., 22/3/1975, *Oliver 5778* (STE).

— 3421 (Riversdale): stony hillside above coast at Puntjie, Riversdale Division (-AC), 18/5/1950, *Esterhuysen 16971* (BOL); Puntjie, sand and limestone hills near coast, 24/1/1961, *Esterhuysen 28753* (BOL); Puntjie, Duiwenhoks River Mouth, 200 ft., 3/9/1973, *Boucher 2229* (PRE); 6.7 miles S.E. of Vermaaklikheid P.O., Riversdale Division, 500 ft., 29/7/1962, *Acocks 22529* (K, PRE); 16 miles S. of Riversdale, 400 ft., 28/7/1968, *Acocks 24011* (K, PRE); Still Bay hills, Riversdale Division, 9/8/1949, *Morris 264* (BOL).

— 3422 (Mossel Bay): Mossel Bay (-AA), -/6/1928, *Salter 371/3* (BM), -/1/1913, *Bro. Moran s.n.* (BOL, PRE, SAM); in campis prope Mossel Bay, -/4/1899, *Bourne s.n.* (SAM 14095); sandy hills near the landing place, Mossel Bay, 18/10/1814, *Burchell 6239* (K); macchia near Golf Course, Mossel Bay, 7/8/1936, *Lindeberg s.n.* (LD 83); hillside along National Road towards George, Mossel Bay Division, 18/1/1964, *Esterhuysen 30608* (BOL); Great Brak River, fixed dunes, George Division, 1/6/1952, *Compton 23541* (BOL); Botha's Strand, 3 km east of Great Brak River Mouth, George Division, 200 ft., 29/10/1971, *Williams 1568* (NBG); Herolds Bay, George Division, 250 ft., 19/6/1977, *Williams 2310* (NBG).

Note: the locality "Genadendal 4 000 ft.", 31/12/1896, *Schlechter 9875* (BM, E, G, GRA, K, P, PH, S, W) is extremely doubtful.

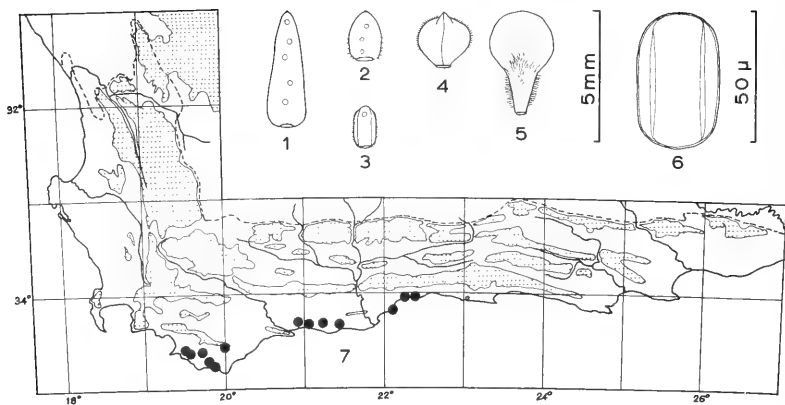


FIG. 3.

Euchaetis burchellii: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, pollen. 7, distribution.

5. *Euchaetis scabricosta* Williams in JI S. Afr. Bot. **40** (4): 286 (1974). Type: CAPE—3420 (Bredasdorp): Potberg, sandy flats on south side of mountain, 3 km from Potberg Farm, Bredasdorp Division (-BC), 19/9/1972, *Williams 1689* (NBG, holotype).

Euchaetis scabricosta is a distinct species having the disc closing over the ovary at first, having fruits with horns not deeply cleft, and having leaves not gibbous behind the apex, opposite and with the midrib prominent, gland-stepped or scabrous.

It differs from *E. burchellii* which has leaves sessile with two rows of gland dots to either side of the midrib, and fruits with shorter horns. It differs from *E. meridionalis* which has a midrib with fewer gland dots, leaves more obtuse, more crowded, shorter and broader, with a resinous exudate towards the leaf axils. *E. scabricosta* is found growing in sandy ground and *E. meridionalis* upon a limestone formation.

6. *Euchaetis meridionalis* Williams in JI S. Afr. Bot. **44** (4): 329 (1978). Type: CAPE—3420 (Bredasdorp): De Hoop behind sand dunes on track to Koppie Alleen, Bredasdorp Division (-AD), 14/4/1972, *Williams 1644* (NBG, holotype).

Euchaetis meridionalis is recognised as distinct having the disc closing over the ovary at first, the fruit 5-carpellate with the horns not deeply cleft, and leaves broadly lanceolate, sub-complicate, glabrous, opposite or alternate on the same plant and not gibbous behind the apex. It differs from *E. scabricosta* having a midrib with fewer gland dots, leaves more obtuse, more crowded, shorter

and broader, with a resinous exudate towards the leaf axils. *E. meridionalis* is found growing only upon limestone whereas *E. scabricosta* grows in sandy soil.

7. ***Euchaetis intonsa*** Williams in Jl S. Afr. Bot. **44** (4): 335 (1978). Type: CAPE—3420 (Bredasdorp): north side of pass from Wydegelegen to De Hoop, at base of limestone hills, on gently sloping ground in crevices and in shallow soil on limestone bedrock (-AD), 100 m (350 ft.), 3/8/1975, Williams 2028 (NBG, holotype; K, MO, NSW, PERTH, PRE, S, STE, isotypes).

Euchaetis intonsa is a distinct species having leaves alternate, elliptic, sparsely pubescent and ciliate, with bracts, bracteoles and calyx lobes pubescent and with petals small with the midrib glabrous inside.

It differs from *E. burchellii*, *E. laevigata* and *E. scabricosta* which have opposite leaves, glabrous bracts and glabrous calyx lobes. Although *E. meridionalis*, a more glabrous plant, is found nearby and may have 4 or 5-ranked leaves, it differs from *E. intonsa* which has smaller, sparsely pubescent leaves and pubescent bracts, bracteoles and calyx lobes.

8. ***Euchaetis ericoides*** Dümmer in Kew Bull.: 91 (1912). Type: without precise locality, received Sept. 1860, Admiral Sir F. Grey (K, holotype).

The fact that no locality was given with Admiral Grey's collection of this plant presented some difficulty and it was only after the type specimen had been received on loan from Kew that any comparison could be made with material in local herbaria. Fortunately the type was found to exactly match a specimen of *Euchaetis*, amongst the *incertae* at the Bolus Herbarium, collected by Miss Esterhuysen in 1953 at Schoongezicht Peak. This rather uncommon plant is to be found only in the mountains of the upper reaches of the Olifants River in the Clanwilliam Division and has been seldom collected. The following description (based upon Williams 2294) amplifies that given by Dümmer, in Latin, in the *Kew Bulletin*.

Shrubs 700 mm tall, fairly erect, slender, diffuse, single-stemmed at base. *Branches* somewhat erect, straight, smooth, glabrescent, without order. *Branchlets* spreading-erect, very slender, thinly and minutely puberulous, alternate or occasionally on young plants opposite, not hidden by the leaves. *Leaves* 6.5–12 mm long, 1.7–2.2 mm broad, lanceolate, acute, straight or sub-second or sub-falcate, glabrous, sub-glaucous, erect or somewhat spreading, alternate or opposite, sessile; apex with a small blunt callus; margins narrowly translucent and serrulate with numerous minute gland dots nearby; adaxial surface flat and smooth; abaxial surface fairly flat with 2 parallel rows of small gland dots along the midrib. *Inflorescence* terminal, normally 3-nate but if leaves opposite then 4-nate; flowers 5 mm diam., white. *Bract* one per flower, 2.7–3.5 mm long, 1.3 mm broad, lanceolate, sub-glaucous: apex with a blunt callus; margins sub-

serrulate above, ciliolate and translucent below; adaxial surface thinly puberulous; abaxial surface glabrous, with a fairly prominent gland-dotted midrib. *Bracteoles* two, 2.5 mm long, 1.2 mm broad, ovate-lanceolate, apex thickened with a blunt callus; margins broadly translucent and ciliolate; adaxial surface puberulous; abaxial surface glabrous, sub-glaucous. *Calyx lobes* five, 2.8–3.1 mm long, 2 mm broad, oblong-elliptic, obtuse, apex with a small blunt elevated callus, margins ciliate and very broadly translucent; abaxial surface pubescent towards the middle; adaxial surface glaucous, glabrous, midrib obscurely gland-dotted. *Petals* five, 5 mm long overall; *limb* 2 mm long, 2 mm broad, orbicular, apiculate-retuse, strongly recurved, white; margin minutely serrulate; *claw* 3 mm long, 1.2 mm broad, strongly transversely bearded above extending mainly down the prominent midrib; margins ciliate. *Staminodes* five, vestigial, a minute green gland at most 0.1 mm long. *Filaments* five, becoming 1.7 mm long after anthesis, subulate, glabrous. *Anthers* five, before anthesis 1 mm long, 0.7 mm broad, wine-coloured; apical gland small oblong-globose. *Pollen* 50 μ long, 30 μ broad, oblong. *Disc* exceeds the ovary by a long way, closing over it slightly, level on top, green, fleshy. *Stigma* 0.6 mm diam., capitate, depressed globose, green. *Style* becoming 1.5 mm long, erect, glabrous. *Ovary* 5-carpellate, 0.8 mm long, 0.8 mm diam., apices minutely scabrid. *Fruit* 5-carpellate, 9.5–10 mm long, 5 mm diam., glabrous, each carpel with a conspicuous wine-coloured stripe down the midrib and with, to either side, margins bearing a gland-dotted ridge; *horns* about 4 mm long, erect with apex retuse and minutely scabrid. *Seed* 5–6 mm long, including a white aril 1.5 mm long, 1.8–2.2 mm broad, black not shining (partly from *Esterhuysen* 21277).

Euchaetis ericoides is recognised as distinct because of having leaves that are rather flat with a tendency to curl upwards, i.e. sub-second. Other distinguishing characters are: the disc closes over the ovary at first, the fruit is 5-carpellate with horns not cleft at the apex, the leaves are lanceolate, fairly flat, glabrous, opposite or alternate and not gibbous behind the apex.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): Schoongezicht Peak, Cold Bokkeveld Mountains, Ceres Division (-CC), -/4/1939, *Stokoe* 7673 (BOL), 3 500–4 500 ft., 4/4/1953, *Esterhuysen* 21277 (BOL), 5/4/1953, *Stokoe s.n.* (SAM 67228), 17/9/1949, *Hanekom* 1232 (PRE); lower slopes of Olifants River Mountains at Thee River, Clanwilliam Division, 17/4/1949, *Esterhuysen* 15338 (BOL); Keerom, stony west slopes of Cold Bokkeveld Mountains above Olifants River valley, Clanwilliam Division, 4/12/1950, *Esterhuysen* 17919 (BOL), 1 900 ft., 24/3/1977, *Williams* 2294 (NBG); Cardouw Pass, east slopes, Clanwilliam Division, 15/9/1953, *Barker* 8126 (NBG), *Lewis* 4138 (SAM).

Without precise locality: *Admiral Sir F. Grey* (K).

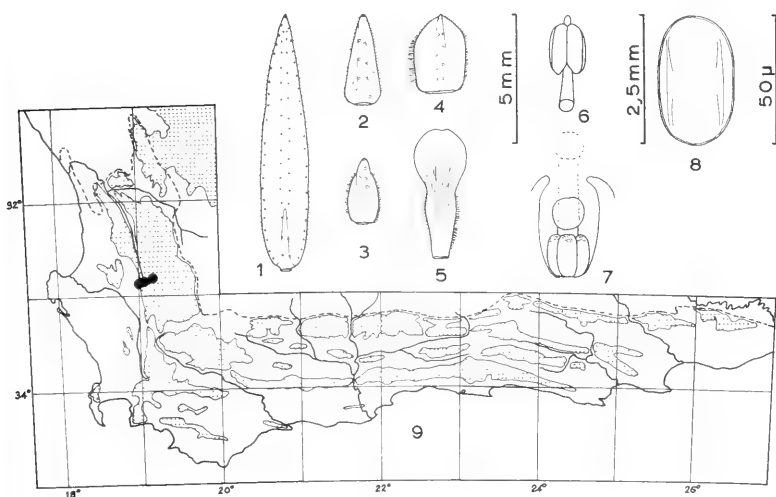


FIG. 4.

Euchaetis ericoides: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

9. *Euchaetis tricarpellata* Williams in JI S. Afr. Bot. **41** (4): 241 (1975). Type: CAPE—3218 (Clanwilliam): south from the summit of Versveld's Pass, Piquetberg Division (-DC), 640 m. 18/9/1972. *Williams 1690* (NBG, holotype).

Euchaetis tricarpellata is recognised as a distinct species because of its three-chambered ovary. All other species in the genus are 5-carpellate.

10. *Euchaetis vallis-simiae* Williams in JI S. Afr. Bot. **45** (2): 156 (1979). Type: CAPE - 3323 (Willowmore): Baviaanskloof Forest Reserve at Studtis, on forestry road at end of first plateau (-DB), 915 m alt., 12/10/1976, *Williams 2224* (NBG, holotype; AD, B, BOL, K, L, M, MO, NSW, PRE, S, STE, isotypes).

Euchaetis vallis-simiae is recognised as distinct because of having prominently-nerved, elliptic leaves which, with the bracts, bracteoles and calyx lobes, are conspicuously gibbous behind the apex and scabro-tomentose on all sides.

It is also useful to note that the disc closes over the ovary at first and that the style is always erect and bears an unusually large stigma.

11. *Euchaetis cristagalli* Williams in JI S. Afr. Bot. **45** (2): 147 (1979). Type: CAPE—3324 (Steytlerville): east of Cockscomb, Great Winterhoek Mtns., Uitenhage Division (-DB), 915–975 m alt., 9/3/1977, *Williams 2283* (NBG, holotype; BOL, K, L, MO, PRE, S, STE, isotypes).



FIG. 5.
Euchaetis ericoides: flower showing bearded petals.

Euchaetis cristagalli is most easily recognised as distinct from other species of *Euchaetis* with linear-lanceolate leaves because of its having the longest petals. It has been observed that these petals very readily fall away. *E. cristagalli* may be distinguished from *E. elata* which has leaves sessile, pubescent on the adaxial surface, and flowers sessile \pm 3-nate, with the style at some time deflexed; from *E. glomerata* which has broader leaves and smaller flowers in multiflorous heads; from *E. flexilis* which has leaves with sacculate apices and broad translucent margins.

It is perhaps nearest in appearance to *E. linearis* which however has leaves with only two rows of gland dots, flowers in many flowered heads with small petals and a disc that stands open, not obvallate.

12. ***Euchaetis avisylvana*** Williams in JI S. Afr. Bot. **44** (4): 339 (1978). Type: CAPE—3320 (Montagu): Grootvadersbos, on a stony south facing shoulder, Heidelberg Division (-DD), 425 m (1 400 ft.) alt., 29/4/1975, Williams 1997 (NBG, holotype; BOL, C, GRA, K, M, MO, NSW, PERTH, PRE, S, STE, isotypes).

Euchaetis avisylvana is distinct on account of having villous-ciliate leaves tipped with a few hairs at the apex; lanceolate-acute, white, somewhat petal-like calyx lobes and acute petals. It differs from *E. elata* E. & Z. which has leaves, bracts, bracteoles and calyx lobes much shorter and ciliate, not villous-ciliate, and also the blade of the petal elliptic-apiculate not lanceolate-acute.

The very short horns on the fruit of *E. avisylvana* at once distinguish it from *E. longicornis* Williams which has leaves, bracts, bracteoles and calyx lobes with very sharp points and with gland dots scattered and not in two straight rows. *E. avisylvana* has been found only in a few places on the south slopes of the Langeberg from Tradouw Pass eastwards for about 17 km at altitudes of from 300–600 m.

13. ***Euchaetis elata*** Ecklon & Zeyher, Enum. Plant.: 104 (1835). Type: In lateribus montium "Hottentotshollandsberge" (altit. 4) prope villam "Grietjesgat" non procul a flumine "Palmietrivier" (Stellenbosch), Jun., Ecklon & Zeyher 819 (SAM, lectotype; C, MEL, S, W, isotypes).

As no specific specimen was indicated in the type description, the collection housed in the South African Museum herbarium at Kirstenbosch, South Africa, has been chosen as the lectotype.

Shrubs up to 1 m tall, slender, standing somewhat above the surrounding Restionaceae, not much branched, single-stemmed at base. *Branches* few in number, rod-like, erect, glabrous, with a smooth grey-brown bark. *Branchlets* few, straight, erect, slender, glabrous, yellowish, well-clothed with leaves. *Leaves* 6–8 mm long, 1–1.3 mm broad, linear-lanceolate, acute, incurved-mucronate, sessile, erect, adpressed, usually not imbricate, alternate; adaxially concave above and pubescent with short bristly hairs bent towards the apex; abaxially convexo-carinate, glabrous with two rows of gland dots; hyaline margins narrow, minutely ciliate. *Inflorescence* terminal without any involucre, with groups of about three sessile florets at the end of the main stem and at the ends of very short branchlets crowded together, those at the apex being the first to bloom. *Bract* one per floret, 2.5 mm long, 1 mm broad, lanceolate, acute, mucronate, hyaline margins ciliate; adaxially concave, sparsely short-pubescent above; abaxially convexo-carinate, glabrous with two rows of gland

dots. *Bracteoles* two, 2,2 mm long, 0,8 mm broad, similar to the bract. *Calyx lobes* five, 2,5 mm long, 1,2 mm broad, oblong, acute, with a small callus at the apex; margins ciliolate, broadly translucent becoming rolled inwards towards the apex; adaxially somewhat pubescent; abaxially glabrous with two rows of gland dots. *Petals* five, 3,8 mm long overall; *limb* 1,3 mm broad, elliptic, minutely apiculate, white, gland-dotted; *claw* 2 mm long, 0,7 mm broad, narrowing below, strongly transversely bearded above, ciliate. *Staminodes* not visible except as a round spot on the disc. *Filaments* five, becoming 1 mm long, subulate, glabrous. *Anthers* five, 0,8 mm long, 0,7 mm broad, plum-coloured; apical gland minute, inflexed. *Pollen* 40 μ long, 20 μ diam., oblong, surface rough-dotted. *Disc* exceeds the ovary, exudes nectar. *Stigma* capitellate, much the same diam., as the style. *Style* at first deflexed, becoming erect, 1,3 mm long, slender, glabrous. *Ovary* 5-carpellate, 0,7 mm diam., glabrous, apices globose. *Fruit* 5-carpellate, 5,5 mm long, 5 mm diam., glabrous, smooth, gland-dotted; horns 0,5–1 mm long. *Seed* 3,8–4 mm long, 2 mm broad, black, shining; aril black.

Euchaetis elata is recognised as distinct having the disc obvallate, surrounding the ovary but neither closing over it nor spreading, having flowerheads without conspicuous involucre leaves as in *E. longibracteata*, with the flowers opening first at the apex of the inflorescence, having the style at some stage deflexed, with petals obtuse 3,8 mm long, not as long as 5,5 mm in *E. cristagalli*, having leaves linear-lanceolate, inflexed, obtusely mucronate, not flat, with margins ciliolate or crisped ciliate, not villous ciliate as in *E. avisylvana*, and having fruits with horns less than 1 mm long not 3,5 mm long as in *E. glomerata*. The leaves of *E. linearis* are seen to differ in having more numerous gland dots that are also very much smaller in diameter, and the leaves of *E. flexilis* clearly differ in their sacculate apices.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Slanghoek mountains, Cossacks, Worcester Division (-CA), 4 000 ft., 7/3/1943, *Esterhuysen* 8626 (BOL); Slanghoek mountains, Witteberg, Worcester Division, 21/11/1943, *Esterhuysen* 9494 (BOL), 5 000 ft., 13/11/1949, *Esterhuysen* 16523 (BOL); Slanghoek Pile, shale band, Worcester Division, -/1/1940, *Esterhuysen* 1728 (BOL); upper Wellington Sneeuwkop, shale band, Paarl Division, 5 000 ft., 8/1/1943, *Esterhuysen* 8645 (BOL), 9/1/1949, *Esterhuysen* 15038 (BOL); Du Toits Kloof, 3 500 ft., 7/6/1897, *A. Bolus s.n.* (BOL, *Guthrie* 4680); Haalhoeksneeuwkop, Paarl Division (-CC), -/4/1942, *Stokoe s.n.* (SAM 59351), -/4/1942, *Esterhuysen* 7714 (BOL, SAM).

— 3418 (Simonstown): In lateribus montium Hottentotshollandsberge procul villam Grietjesgat non procul a flumine Palmietrivier, Caledon Division (-BB), 1 500–2 000 ft. alt., -/6/-, *Ecklon & Zeyher* 819 (SAM, C, MEL, S, W); between Sir Lowry's Pass and Elgin, 12/4/1941, *Compton* 10660 (NBG); Kogelberg, S.E. slopes, 3 000–4 000 ft., 16/1/1944, *Esterhuysen* 9990 (BOL); Kogelberg Forest

Reserve boundary with Somersfontein, 274 m, 15/4/1970, *Boucher* 1230 (STE); Arieskraal, west side of Palmiet River, rocky places, 800 ft., 12/2/1973, *Williams* 1757 (NBG); Palmiet River, Oudebos (-BD), 19/4/1966, *Esterhuysen* 31523 (BOL).

— 3419 (Caledon): Elgin, Caledon Division (-AA), 24/4/1943, *Compton* 14488 (BOL, NBG); Palmiet River, Elgin, 28/2/1942, *Stokoe* 8497 (BOL, K, NBG, SAM 59349), -/1/1943, *Stokoe* 8498 (BOL, K); Palmiet River, Grabouw, -/12/1942, *Stokoe* (SAM 59348); mountain slopes east and west of Palmiet River, Elgin, 25/4/1943, *Leighton* 313 (BOL, K); Viljoens Pass, south side, -/8/1946, *Sidey* 2405 (S), -/8/1946, *Stokoe s.n.* (S, SAM 59347), 1 650 ft., 15/4/1975, *Williams* 1996 (NBG); Hottentotsholland Mtns., between Somerset Sneeuwkop and Dwarsberg, -/9/1946, *Stokoe s.n.* (G, SAM 59346).)

DISTRIBUTION AND VARIATION

Euchaetis elata appears to have a north-south distribution in the mountains of the south west Cape, extending from near the mouth of the Palmiet River in the Caledon Division northwards to the Slanghoek mountains in the Worcester Division a distance of about 8 km at altitudes varying from about 200 to 1 500 metres.

Towards the north, where the populations occur at higher altitudes, plants appear to have broader distinctly petiolate leaves with the margins becoming crisped ciliate; on the broadest leaves two extra rows of gland dots appear along the margins, one to either side. Young leaves become decidedly pubescent in the most northerly populations and the sparse pubescence on the adaxial surface of the leaves seems to disappear.

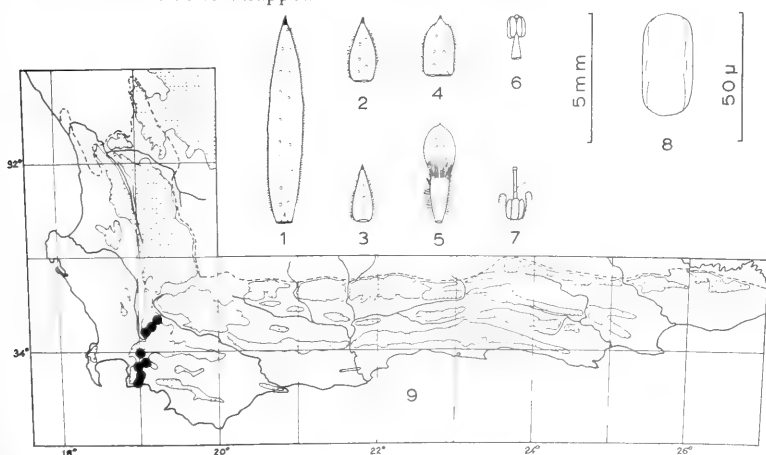


FIG. 6.

Euchaetis elata: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.



FIG. 7.

Euchaetis elata: flowerhead showing youngest flowers at the perimeter.

14. *Euchaetis glomerata* Bartling & Wendland, Diosmeae in Beitr. Bot. 1: 16 (1824). Type: ad Cap. b. Spei, Hesse (GOET-BARTL, lectotype; GOET, isotype, as to specimen no. 2 on R.H. side).

Euchaetis abietina Eckl. & Zeyh., Enum. Plant.: 104 (1835). Type: in nemoribus (alt. 1 500–2 000 ft.) ad montes "Cederberge" (Clanwilliam), -/6/-, Ecklon & Zeyher 821 (C, G, GOET, K, MEL, P, PRE, SAM, W).

Diosma glomerata G. F. W. Mey. mss. nom. nud.

As this was the only species of *Euchaetis* known to Bartling and Wendland when they proposed the new genus *Euchaetis* in 1824, it must be regarded as the type species of the genus. The specimen in Bartling's herbarium which he received in 1820 is chosen as the lectotype and another rather more typical twig received in 1836 from G. F. W. Meyer is therefore an isotype. The following description made from fresh material complements the very detailed description in Latin of Bartling & Wendland.

Shrubs 0,2–0,4 m tall, lax, diffuse, growing amongst Restionaceae, often branching from near the base. *Branches* slender, lax, seldom numerous, soon leafless, smooth, greyish to reddish-brown. *Branchlets* erect, very slender, rod-like, glabrous, mostly hidden beneath the leaves, reddish where exposed. *Leaves* 4,3–8,5 mm long, 1,3–1,7 mm broad, lanceolate, acute, somewhat incurved mucronate, glabrous, sessile, alternate, adpressed, sub-imbricate, more crowded beneath the head; adaxially concave; abaxially round-keeled with gland dots to

either side of the midrib; margins narrowly translucent, ciliate or ciliolate-serrulate with occasionally one or two gland dots. *Inflorescence* terminal, about 8 mm diam., glomerate consisting of up to \pm 15 florets, those at the apex opening latest, those at the base aborting and falling away. *Bract* 1.9–2.5 mm long, 1.1 mm broad, oblanceolate, acute, mucronate, glabrous, gland-dotted; margins narrowly translucent, ciliate. *Bracteoles* two, 1.5–1.9 mm long, 0.7 mm broad, asymmetrical, acute or sub-obtuse, apex minutely callused, glabrous, gland-dotted; margins broadly translucent, ciliolate. *Calyx lobes* five, 2–2.5 mm long, 1.1–1.3 mm broad, oblong-lanceolate, apex acute deflected, minutely rough-callused; midrib minutely gland-dotted in two rows; margins ciliolate, translucent. *Petals* 2.7–2.8 mm long overall, white; *limb* 1.1–1.2 mm long, 0.6–1.0 mm broad, glabrous, oblong; *claw* 1.5–1.7 mm long, 0.9–1.2 mm broad, transversely bearded above, margins ciliate. *Staminodes* not visible. *Filaments* five, becoming 1–1.2 mm long, glabrous, acicular. *Anthers* five, 0.7–0.9 mm long, 0.6–0.7 mm broad, wine-coloured; apical gland minute, white, globose. *Pollen* 45 μ long, 18 μ broad, oblong, slightly waisted. *Disc* sinuate, level on top, closely surrounds the ovary and exceeds it, purplish, exudes nectar. *Stigma* 0.2–0.3 mm diam., capitellate. *Style* becoming 1 mm long, deflexed at first, glabrous. *Ovary* 5-carpellate, 1.1 mm long, 0.8 mm diam., glabrous, apices globose. *Fruit* 5-carpellate, 8–12 mm long overall, 7 mm diam., glabrous, reddened; horns 2–4.5 mm long, spreading slightly. *Seed* 6 mm long, including the black-streaked aril, 2.1–2.7 mm broad, black, matt.

E. glomerata is recognised as distinct having the disc obvallate, neither closing over the ovary nor spreading, having the style at some stage deflexed and petals obtuse only 2.8 mm long, having leaves lanceolate, acute, sessile, adpressed, with margins serrulate and rigidly ciliate, and having fruits with horns 3.5 mm long. In the flowerheads the first flowers open at the base of the head and the last at the apex. The opposite occurs in *E. elata*. It possesses no conspicuous involucreal leaves as in *E. longibracteata*, the leaves are not villous ciliate as in *E. avisylvana* and not sacculate at the apex as in *E. flexilis*.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): Pakhuis mountains, Clanwilliam Division (-AA), 28/12/1941, *Esterhuysen* 7409 (BOL); Cedarberg near Krakadouw Pass, 3 000 ft., 8/10/1897, *Bodkin* s.n. (BOL 8955); Cedarberg, Middelberg (-AC), 4 000 ft., 24/9/1930, *Barnes* s.n. (BOL 19474), 16/12/1941, *Esterhuysen* 7281 (BOL), 15/12/1941, *Esterhuysen* 7364 (BOL, NBG), 3/1/1942, *Esterhuysen* 7600 (BOL), 6/10/1946, *Esterhuysen* 13022 (BOL), 25/9/1937, *Lewis* s.n. (BOL), 4 000 ft., 25/9/1937, *Compton* 7044 (BOL, NBG), 2 500 ft., 18/5/1966, *Taylor* 6833 (PRE); Cedarberg, Boschkloof, 4 000 ft., 14/10/1923, *Pocock* 239 (STE); Cedarberg, *Zeyher* s.n. (S), -/11/1939, *Stokoe* 7608 (BOL); Cedarberg, shale band w. side of path to Tafelberg, 4 000 ft., 24/4/1942, *Esterhuysen* 8080 (BOL);

in nemorosis ad Cedarmountains, Clanwilliam, 1 500–2 000 ft., *Ecklon 1035* (= *E. & Z.821*) (C, G, GOET, K, MEL, P, PRE, S, SAM, W); Cedarberg, upper slopes near Algeria, 24/10/1930, *Galpin 10580* (PRE), –/3/1940, *Stokoe s.n.* (SAM 58832); Cedarberg, N.W. end of Langeberg, 5 300 ft., 15/2/1973, *Williams 1765* (NBG); Sneeuwberg hut area, 4 500–5 000 ft., *Taylor 5129* (PRE), 4 250 ft., 1/12/1976, *Williams 2248* (NBG); Sneeuwberg shale band, 5 500 ft., 16/5/1966, *Taylor 6820A* (STE); south slope of Elandskloof, Clanwilliam Division (-CA), 4 000 ft., 3/10/1940, *Esterhuysen 3148* (BOL, NBG); Donkerkloof Peak, near Citrusdal, –/1/1945, *Stokoe 9143* (BOL, SAM 59342); S. Cedarberg, shale band E. of Sneeuwberg, 5 000 ft., 10/10/1946, *Esterhuysen 13079* (BOL); S. Cedarberg, shale band at head of Krom River kloof, 5 000 ft., 11/12/1950, *Esterhuysen 18032* (BOL); Baths Mountains, Clanwilliam Division, 2 000 ft., 8/7/1935, *Compton 5376* (NBG); Cedarberg, Duivelskloof, –/9/1950, *Stokoe s.n.* (SAM 64145); Apex Peak, S. Cedarbergen, 3 000–4 000 ft., 1/4/1961, *Esterhuysen 28946* (BOL); S. Cedarberg, ridge S. of Krom River (-CB), 3 600 ft., 18/9/1975, *Williams 2084* (NBG), 4/10/1952, *Esterhuysen 20502* (BOL); Schoongezicht Peak, Ceres Division (-CC), –/4/1939, *Stokoe 7672* (BOL), 3 500–4 500 ft., 4/4/1953, *Esterhuysen 21295* (BOL), –/4/1939, *Stokoe s.n.* (SAM 54205), 5/4/1953, *Stokoe s.n.* (SAM); Vredelus, E. base of Schoongezicht Peak, 2/9/1962, *Esterhuysen 29673* (BOL), 21/4/1973, *Esterhuysen 33171* (BOL); lower slopes of mountains at Thee River, 17/4/1949, *Esterhuysen 15337* (BOL); Keerom, stony W. slopes, 4/12/1950, *Esterhuysen 17918* (BOL), 1 900 ft., 24/3/1977, *Williams 2299* (NBG).

—3319 (Worcester): slopes of Witsenberg, Tulbagh Division (-AA), –/9/1939, *Esterhuysen 2640* (BOL, K); Sneeuwgat, Great Winterhoek Mountains, Tulbagh Division, 4 000–5 000 ft., 30/12/1951, *Esterhuysen 19749* (BOL); Saronsberg, Tulbagh Division, 2 000–2 500 ft., 17/1/1965, *Esterhuysen 30933* (BOL); Twenty-four Rivers Mountains above Porterville, Piketberg Division, 22/10/1949, *Esterhuysen 16412* (BOL, K); Witsenberg Vlake a few miles before Visgat, Ceres Division, 2 000–3 000 ft., 11/1/1960, *Esterhuysen 28402* (BOL); Cold Bokkeveld Mountains near Visgat, 16/12/1946, *Esterhuysen s.n.* (BOL); Visgat, 913 m, 15/5/1975, *Williams 1998* (NBG); Boboskloof, ridge S. of ruin, 980 m, 22/11/1975, *Williams 2149* (NBG); rocky slopes in Schurftteberg Pass, Ceres Division (-AB), 30/7/1950, *Esterhuysen 17378* (BOL, NBG); Ceres Peak, slopes above Michells Pass (-AD), 24/5/1941, *Esterhuysen 5198* (BOL, NBG); Slab Peak, Michells Pass, 4 000 ft., 5/10/1941, *Esterhuysen 6171* (BOL, NBG); slopes below Castle Rocks, Michells Pass, 16/11/1947, *Esterhuysen 14149* (BOL), 5/12/1948, *Esterhuysen 14713* (BOL), 9/11/1952, *Esterhuysen 20709* (BOL); Michells Pass, half a mile from the summit, 1 600 ft., 20/3/1975, *Williams 1984* (NBG); W. of the summit of Michells Pass, 1 900 ft., 15/5/1975, *Williams 2001* (NBG); Ezelsfontein, rocky lower slopes of Milner Peak, 1/9/1952, *Esterhuysen 20363* (BOL); Schurftteberg, N. of Bertsberg, 8/10/1953, *Esterhuysen 21865* (BOL).

DISTRIBUTION AND VARIATION

Euchaetis glomerata has been found growing in soil derived from the Table Mountain Sandstone in stony or rocky places from Pakhuis Mountain near Clanwilliam in the north to the vicinity of Michells Pass near Ceres in the south, a distance of about 145 km. at altitudes of from 488 to 1 676 m (1 600 to 5 500 ft.) above sea level. Flowering appears to take place throughout the year and ripe fruits have been collected from September until February.

Some variation can be seen in leaf size. Populations with smaller leaves appear to have the bracts and calyx lobes more obtuse. Plants from the Wemmershoek Slanghoek mountains once thought to belong to this species are apparently quite different having leaves petiolate much broader and more crowded with ciliate margins.

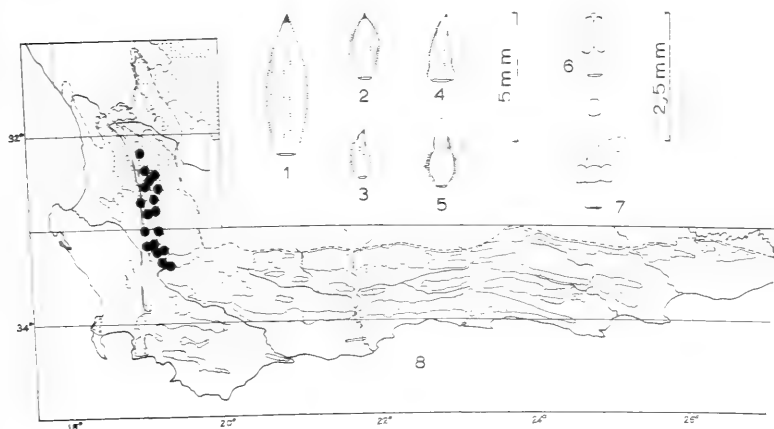


FIG. 8.

Euchaetis glomerata: 1. leaf. 2. bract. 3. bracteole. 4. calyx lobe. 5. petal. 6. anther. 7. gynoeceium. 8. distribution.

15. *Euchaetis flexilis* Ecklon & Zeyher, Enum. Plant.: 105 (1835). Type: Ad montem "Baviaansberg" prope "Genadenthal" (altit. 1 500–2 000 ft.) Caledon. –(7)–, Ecklon & Zeyher 822 (SAM, lectotype: C. MEL. S. isotypes).

Euchaetis roilophylla Schltr. nom. nud.

The mission station at Genadendal in the Caledon District was a favourite stopping place for travellers in the early days and it was here that *E. flexilis* was first discovered by Ecklon or Zeyher. As the whereabouts of the actual specimen used by the authors in their description is unknown, a specimen preserved in the herbarium of the South African Museum at Kirstenbosch is now chosen as the lectotype of *Euchaetis flexilis* E. & Z.



FIG. 9.

Euchaetis glomerata: flowerhead showing youngest flowers at the apex.

Shrubs 0,2–0,4 m tall, slender, branching from near the base, may survive fires. *Branches* slender, lax, glabrous, smooth. *Branchlets* very slender, somewhat erect, well-clothed with leaves. *Leaves* 4–6 mm long, 1,5–2,3 mm broad, oblong-elliptic, obtuse, glabrous, adpressed to imbricate, opposite or alternate, sessile; apex sacculate; margins minutely ciliolate and broadly translucent; adaxial surface concave; abaxial surface rounded, conspicuously gland-dotted. *Inflorescence* terminal, with about 6 florets in a reduced compound raceme; *flowers* about 5 mm diam., white. *Bract* one to each flower, 2,8 mm long, 1,6 mm broad, elliptic, obtuse, glabrous; margins ciliolate, broadly translucent. *Bracteoles* two, 2 mm long, similar to the bract but smaller. *Calyx lobes* five, 2–2,5 mm long, 1,5 mm broad, elliptic, obtuse, reddened, gland-dotted; margins ciliolate, broadly translucent. *Petals* five, 3,2–3,6 mm long, 1,3–1,8 mm broad, cuneate-obtuse, white, transversely bearded and ciliate in the middle, narrowing below to 0,5 mm at the base. *Staminodes* five, vestigial, a minute almost submerged hemispherical dot. *Filaments* five, becoming 1 mm long, glabrous. *Anthers* five, about 1 mm long before anthesis; apical gland 0,12 mm diam., minute. *Disc* sinuate, red, exudes nectar, fairly level on top, exceeds the ovary by a small amount. *Stigma* 0,2 mm diam., depressed globose, capitellate. *Style* glabrous, at first deflexed, becoming 1,2 mm long, erect after the petals have fallen at which stage unfertilised flowers fall off. *Ovary* 5-carpellate, carpels ovoid obtuse, glabrous. *Fruit* 5-carpellate, 4,5 mm long, 4,2 mm diam., carpels glabrous, reddened, without gland dots, 2-ribbed towards the apex; horns 0,7

mm long, very short, dark red, somewhat spreading with an immersed gland towards the apex. Seed 2.8–3.2 mm long, 1.7–1.9 mm broad, black, shining; aril black.

Euchaetis flexilis is recognised as distinct having the disc obvallate not closing over the ovary and not spreading, having no involucre leaves, having the style at some stage deflexed, having petals only 3.6 mm long obtuse and having leaves obtuse with the apex sacculate with margins not villous ciliate but minutely ciliate and broadly translucent. Sonder observed "easily known by its smaller leaves with a wide hyaline margin, laxer inflorescence, and more obtuse calyces & bracts".

SPECIMENS EXAMINED

CAPE—3319 (Worcester): du Toits Peak, N.E. ridge, Worcester Division (-CA), 3 000 ft., 6/10/1951, *Esterhuysen 18909* (BOL); Brandvalleiberg, Worcester Division (-CB), 2/6/1940, *Esterhuysen 1926* (BOL), *P. Bond 369* (NBG); Stettynsberg, E. slopes, Worcester Division (-CD), 3 000–4 000 ft., 31/7/1949, *Esterhuysen 15609* (BOL), -/7/1949, *Stokoe s.n.* (SAM 64142); Jonaskop, between F.M. Tower and summit, Worcester Division (-DC), 5 200 ft., 15/3/1975, *Boucher 2734* (STE); N. slopes of Jonaskop near Radio Mast, 4 800 ft., 8/4/1971, *Kruger 1195* (STE); E. slopes of Wildepaardeberg, -/4/1920, *Andrae 341* (STE); Jonaskop N. side, 5 000 ft., 19/10/1971, *Esterhuysen 32688* (BOL); Road to Jonaskop, Wildepaardeberg, 3 400 ft., 19/10/1971, *Williams 1559* (NBG); Omklair, Robertson Division, -/2/1940, *Stokoe 7674* (BOL).

— 3419 (Caledon): On Donkerhoekberg, Caledon Division (-AB), 9/3/1815, *Burchell 7967* (K); Nooitgedacht, W. of Genadendal, 1 500 ft., 19/10/1976, *Williams 2228* (NBG); Genadendal in montibus, Caledon Division (-BA), 3 500 ft., 3/4/1897, *Schlechter 10324* (BM, BOL, G, GRA, K, PRE), 3 000 ft., 1/4/1897, *Schlechter 10295* (G, P, S); in monte Baviaansberg, Genadendal, -/7/-, *Ecklon and Zeyher 822* (SAM, lectotype; C, MEL, S, isotypes); in the ascent of the great mountain of Baviaansklouf at Genadendal, 15/2/1815, *Burchell 7653* (K, GRA, P, W); Skilpadkop, Riviersonderend Mtns., Caledon Division (-BA), 13/4/1941, *Compton 10670* (BOL, NBG), *Esterhuysen 5051* (BOL, K, NBG, SAM), 2 500–3 000 ft., 30/11/1952, *Esterhuysen 20783* (BOL), 3 000 ft., 2/1/1953, *Esterhuysen 21043* (BOL); Canonkop, Riviersonderend Mtns. above Genadendal, 3 500–4 000 ft., 21/2/1966, *Esterhuysen 31463* (BOL); Galgeberg near the Post Office Tower, Robertson Division, 4 500 ft., 2/5/1971, *Thompson 1152* (STE); Galgeberg, 3 500 ft., 23/3/1972, *Williams 1628* (NBG); Galgeberg summit, 4 600 ft., 4/2/1975, *Williams 1962* (NBG), 10/8/1975, *Williams 2040* (NBG); Riviersonderend, Caledon Division (-BB), -/4/1930, *Stokoe 2120* (BOL, STE), 2139 (BOL, K), 2 000 ft., -/9/1943, *Stokoe 8861* (BOL), 30/4/1950, *Midlemost 1666* (NBG), -/5/1950, *Lewis & Davis s.n.* (SAM 59353); Rivierson-

derend Peak, 3 000–4 000 ft., 2/9/1951, *Esterhuysen 18750* (BOL, K, LD); Riviersonderend, Pilarkop, 900–1 000 m, 13/12/1965, *Dahlgren & Strid 4549* (K, LD, S), 3 000–4 000 ft., 17/11/1965, *Esterhuysen 31392* (BOL).

DISTRIBUTION

Euchaetis flexilis has been found mainly in the mountains of the Riversonderend Range from Donkerhoek in the west to Pilarkop above the town of Riviersonderend in the east with outliers extending into the Stettynsberg and the Du Toits Kloof mountains towards the north. It grows at altitudes of 600 to 1585 m (2 000 to 5 200 ft.).

VARIATION

In the centre of the distribution range on north-facing slopes in the vicinity of Jonaskop and Galgeberg, plants may be found with much broader leaves in which the gland dots are more conspicuous. These plants have been seen to be growing in rock crevices and this may be a factor affecting this odd character. R. Schlechter gave the manuscript name *E. roilophylla* to these plants.

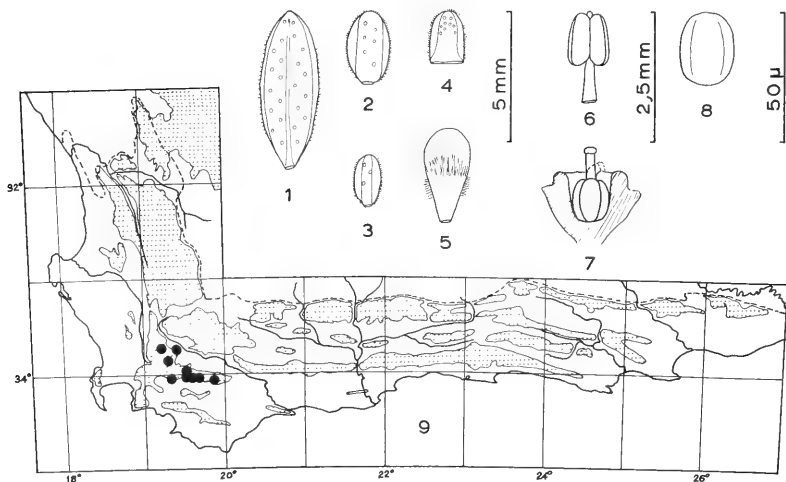


FIG. 10.

Euchaetis flexilis: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

16. **Euchaetis glabra** Williams in Jl S. Afr. Bot. **39** (3): 229 (1973). Type: CAPE—3418 (Simonstown): on a N.E. ridge of the Kogelberg, 5,3 km due south of Sir Lowrys Pass summit, Caledon Division (-BB), 807 m alt., 10/6/1962, Williams 1654 (NBG, holotype; K, MO, M, PRE, S, STE, isotypes).

Euchaetis glabra is recognised as distinct on account of its having orbicular-elliptic petiolate leaves with thin margins and in its being completely glabrous.

17. **Euchaetis longibracteata** Schlechter in Bot. Jb. **24**: 438 (1898). Type: Western Cape: on stony hills near Elim, 80 m above sea level, flowering in April 1896, Schlechter 7627 (BOL, lectotype; BM, K, P, PRE, W, isotypes). Note: see note on typification by Williams in Jl S. Afr. Bot. **40** (4): 281 (1974).

Euchaetis bolusii Dümmer in Kew Bull.: 90 (1912). Type: Cape Colony: Bredasdorp Division; on hills near Bredasdorp, 90 m, Bolus 8473 (K).

Euchaetis radiata Dümmer in Kew Bull.: 91 (1912). Type: Cape Colony: Bredasdorp Division; on hills near Elim, 60 m, Bolus 8532 (K).

The following description, done from fresh material, amplifies those given by previous authors Schlechter and Dümmer.

Shrubs 0,2–0,8 m tall, with several branches arising from a single stem at ground level. *Branches* erect, clustered or forked, glabrous, becoming leafless; bark smooth, brown. *Branchlets* erect, slender, clustered, puberulous, pale or tinged with red, well-clothed with leaves but not hidden. *Leaves* 9,5 mm long including the petiole 1 mm long, 2,5–3 mm broad, lanceolate-oblong, acute, erect or spreading, incurved above, alternate, margins thick, scattered with spiky hairs; narrowed at the base to a short puberulous petiole; adaxial surface glabrous, flat; abaxial surface glabrous, scabrid, pubescent or smooth with or without minute gland dots; midrib prominent with short spiky hairs. *Inflor-escence* terminal, aggregate, conspicuously involucre; florets solitary or several on much reduced branchlets at the perimeter, pink, maturing from the centre outwards, many aborting, only one in each head may eventually ripen and produce seed. *Involucral leaves* conspicuous, crowded, longer than the stem leaves varying in length up to about 15 mm long and in breadth, the innermost becoming almost filiform, linear, acute, almost mucronate, long petiolate, pale or whitish and glabrous on the upper surface, the under surface green towards the apex and clothed with a minute erect pubescence; margins minutely ciliate. *Bract* one to each floret, varying from the outermost 12 mm long, linear-ob lanceolate, green-tipped, to the innermost 3 mm long, tapering, acute, pale, ciliate, withering towards the apex. *Bracteoles* two, 1 mm long, 0,5 mm broad, lanceolate, acute, ciliate, glabrous or puberulous, translucent. *Calyx lobes* five, 2–2,5 mm long, 1,1 mm broad, lanceolate, acute, glabrous or puberulous, ciliate, translucent, reddened below. *Petals* five, 2–3 mm long, 0,7 mm broad, pink; *limb* 1 mm long, 0,6 mm broad, oblong, glabrous, apiculate; *claw* 2 mm long, 0,7 mm broad, elliptic, transversely bearded above, margins ciliate at the sides. *Stami-*

nodes five, vestigial, 0,1 mm long at the outer base of the disc. *Filaments* five, becoming 0,8–1,1 mm long, acicular, glabrous. *Anthers* five, before anthesis 1,1 mm long, 0,7 mm broad, wine-coloured; apical gland 0,1–0,12 mm diam., globose. *Pollen* 42–44 μ long, 18–20 μ broad, oblong. *Disc* 5-sinuate, scarcely exceeds the ovary, does not close over it, dark green, exudes nectar. *Stigma* 0,2 mm diam., capitellate, green. *Style* at first deflexed, becoming 1,4 mm long, glabrous. *Ovary* 5-carpellate, 0,7 mm diam., apices obtuse, rugulose, reddened. *Fruit* 5-carpellate, 6 mm long, 4,3 mm diam., calyx lobes persisting, the base of the calyx forming a pedicel 1,5 mm long, glabrous; gland dots inconspicuous, few; horns erect, short, entire. *Seed* 3,8–4,2 mm long, 1,5 mm broad, black, shining; aril mostly black.

Euchaetis longibracteata with its conspicuous involucre leaves is easily recognised as distinct. It should be noted that it falls into the group in which the disc is obvallate, not closing over the ovary and not spreading.

SPECIMENS EXAMINED

CAPE—3419 (Caledon): on stony hills near Elim, Bredasdorp Division (-DB), 80 m alt., 20/4/1896, *Schlechter* 7627 (BM, BOL, E, G, GRA, K, P, PRE, S); in collibus Rietfontein Poort prope Elim, 200 ft., 10/12/1896, *H. Bolus* 8532 (BOL, K), N. side, 120 ft., 11/1/1972, *Williams* 1623 (NBG), S. side, 150 ft., 11/1/1972, *Williams* 1624 (NBG); in collibus prope Elim, -/12/1896, *H. Bolus* 8531 (BOL), -/7/1895, *H. Bolus* 8478 (BOL), 300 ft., -/4/1897, *Schlechter* 1817 (K, P, SAM 30531); The Poort between Bredasdorp & Elim, 22/4/1933, *L. Bolus* s.n. (BOL 20528, K), 24/1/1948, *Barker* 5264 (BOL, NBG), 1/6/1947, *Compton* 19559 (BOL, NBG), 12/2/1951, *Compton* 22607 (NBG), 500 ft., 12/1/1968, *Williams* 1157 (NBG), -/1/1948, *Lewis* 3099 (SAM), 200 ft., 11/1/1972, *Williams* 1618 (NBG); hills near Bredasdorp, 300 ft., -/7/1895, *H. Bolus* 8473 (BM, BOL, K), 500 ft., -/7/1895, *F. Guthrie* 3873 (BOL, NBG), 15/10/1951, *Esterhuysen* 19133 (BOL, K, NBG); Hangnes farm, Soetanysberg, 400 ft., 28/12/1967, *Rourke* 1010 (NBG, STE), 300 ft., 11/1/1972, *Williams* 1622 (NBG).

— 3420 (Bredasdorp): Vanderstelskraal, Bredasdorp Division (-AC), 450 ft., 2/7/1972, *Williams* 1664 (NBG); near De Hoop vlei, Bredasdorp Division (-AD), 8/1/1950, *Taylor* 90 (BOL); De Hoop, 8/4/1957, *Barker* 8684 (BOL, NBG); at base of hills above De Hoop, 150 ft., 15/4/1972, *Williams* 1645 (NBG); 2 miles S. of Wydelegen P.O., 500 ft., 17/12/1962, *Acocks* 23174 (PRE); Potberg Estates S. of Hamerkop, Swellendam Division (-BC), 300 ft., 1/1/1971, *Oliver* 3226 (K, S); Elandspad farm on road to Stillegat, Swellendam Division, 450 ft., 12/4/1972, *Williams* 1640 (NBG); Cupidos Kraal, Potberg, Bredasdorp Division, 650 ft., 2/7/1972, *Williams* 1666 (NBG), 600 ft., 22/1/1975, *Williams* 1956 (NBG); 3,3 km S. of Potberg farm, Bredasdorp Division, 500 ft., 21/11/1973, *Williams* 1871 (NBG); Cape Infanta, Swellendam Division (-BD), 22/1/1948,

Blum 272 (E); Bredasdorp (-CA), -/4/1927, *Dix s.n.* (SAM 41925); 1.2 miles N.W. of Arniston, 14/12/1962, *Acocks* 23141 (K, PRE).

DISTRIBUTION

E. longibracteata is found growing in pockets of soil upon limestone hills of the Bredasdorp series from Cape Infanta in the east to Rietfontein Poort at the end of the Soetanytsberg in the west; a distance of approximately 100 km. In the vicinity of Rietfontein Poort and Hangnes Farm populations are found in level ground at the base of the limestone hills.

VARIATION

The abaxial leaf surface shows considerable variation and may be glabrous, scabrid, pubescent or smooth, with or without minute gland dots. Bracts, bracteoles, calyx lobes and petals may also vary somewhat in shape and degree of pubescence. The number of florets in each head is also very variable. Leaves may be somewhat spreading or erect and vary in shape and staminodes may sometimes be produced as a very slender filament. In one population the florets were seen not to open widely although the involucre leaves were spreading and conspicuous. Nearby a population was found where the petals became recurved but the involucre leaves remained somewhat closed. There is no explanation for this variability and the question remains as to whether this population may be cleistogamous.

The fact that *E. longibracteata* is found associated with the fairly recent Bredasdorp limestone and also that it is the only species in the sub-family *Diosmeae* to possess conspicuous involucre leaves may indicate that it is one of the more advanced species in the genus.

18. *Euchaetis esterhuyseniae* Williams in JI S. Afr. Bot. **45** (2): 150 (1979). Type: CAPE—3219 (Wupperthal): ridge S.E. of Bloukop, E. Cold Bokkeveld, Ceres Division (-CB), 1 450–1 550 m alt., 18/5/1977, *Williams* 2304 (NBG, holotype; BOL, K, L, MO, PRE, S, STE, isotypes).

Euchaetis esterhuyseniae is recognised as distinct having leaves small, ovate, glabrous, sessile, alternate and spreading, and small flowers with petals that soon fall away. Furthermore the disc is obvallate, the involucre leaves absent, the style at some stage deflexed, the petals 2.5–3 mm long and obtuse, the leaves neither villous ciliate nor sacculate but obtuse, fleshy and spreading.

19. *Euchaetis elsiae* Williams in JI S. Afr. Bot. **40** (2): 85 (1974). Type: CAPE—3219 (Wupperthal): on a ridge S.E. of Bloukop, Cold Bokkeveld, Ceres Division 1 340–1 400 m alt., 8/6/1973, *Williams* 1817 (NBG, holotype; BOL, C, K, M, MO, PRE, S, STE, isotypes).

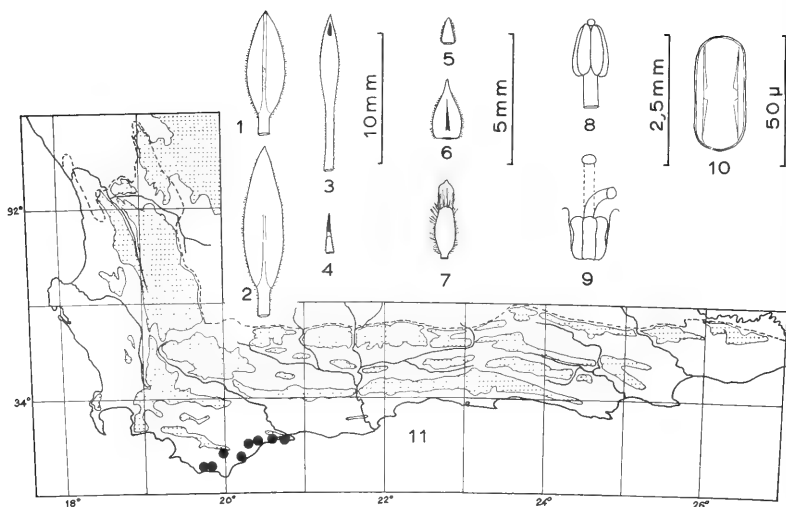


FIG. 11.

Euchaetis longibracteata: 1, leaf. 2, involucre leaf. 3, outermost floral bract. 4, innermost floral bract. 5, bracteole. 6, calyx lobe. 7, petal. 8, anther. 9, gynoecium and disc. 10, pollen. 11, distribution.

Euchaetis elsiae is recognised as distinct on account of its having linear elliptic obtuse leaves, somewhat thickened at the apex, flat on the adaxial surface (concave when dried) and rounded on the outside, with the flowers borne usually in pairs. It differs from *E. glomerata* Bartl. & Wendl., *E. elata* E. & Z., *E. linearis* Sond. and *E. flexilis* E. & Z., all of which have flowers aggregated into multiflorous heads and leaves varying from linear to lanceolate. It is nearest to *E. flexilis* but differs in that the apex of the leaf in *E. elsiae* is thickened whereas in *E. flexilis* it is sacculate.

ADDITIONAL SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): Die Trap/Schurveberg, Cold Bokkeveld, Ceres Division (-CD), 4 700–4 800 ft., 8/12/1976, *Williams* 2256 (NBG).

— 3320 (Montagu): Pypsteelfontein near the beacon, Waboomsberg, Montagu Division (-CA), 4 400 ft., 5/2/1975, *Williams* 1970 (NBG); Waboomsberg on road to Pypsteelfontein, 4 200 ft., 6/2/1975, *Williams* 1971 (NBG); Pienaarspoort, east side, Ceres Division (-AA), 3 200–3 300 ft., 23/7/1975, *Williams* 2022 (NBG).

— 3321 (Ladismith): rocky slope at S.W. base of Peak Wood, Ladismith Division (-AD), 29/3/1959, *Esterhuysen* 28253 (BOL).

DISTRIBUTION

More recent collections from Pienaarspoort near Touws River, from the Waboomsberg near Montagu and from the Swartberg near Ladismith have considerably extended the range of this species towards the east.

VARIATION

In addition to notes made on variation in 1974, when the name was published, it was found that one population of *E. elsiae* from the Waboomsberg in the Montagu Division possessed flowers with beardless petals (Williams 1971). This deficiency is apparently unique and has not so far been observed in any other species in the genus.

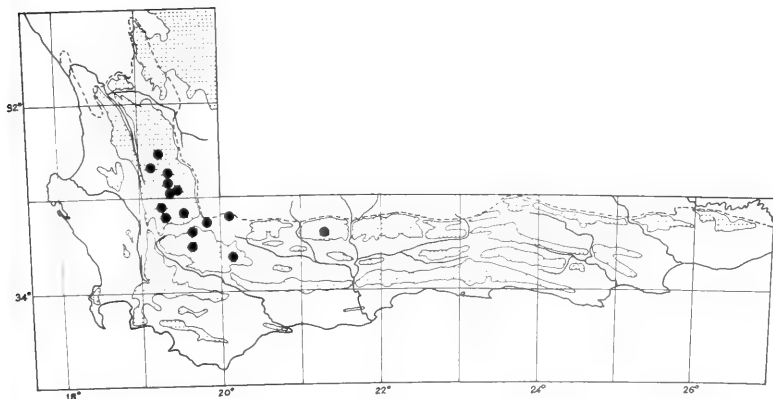


FIG. 12.
Euchaetis elsiae: distribution.

20. ***Euchaetis linearis*** Sond. in Flor. Cap. 1: 372 (1860). Type: In grassy places at the Zwartberg, near Caledon Bath, July. Ecklon & Zeyher 820 (S, lectotype; MEL, S, SAM, isotypes).

It is very often impossible to determine whether Ecklon or Zeyher actually made a collection of material cited under their joint names but in this case a collection by Zeyher, in the South African Museum Herbarium at Kirstenbosch, labelled *Zwartberg July* is probably an isotype and may indicate that in this instance the type material was gathered in July by Zeyher at Caledon. The following description, made from fresh material collected from the type locality, amplifies that of Sonder published in 1860.

Shrubs up to 0.4 m tall, erect, very slender, single-stemmed at base. *Branches* very few, straight, erect, very slender, glabrous, with a smooth reddish-

brown bark. *Branchlets* few, straight, erect, very slender, glabrous or very sparsely puberulous, well-clothed with leaves. *Leaves* 6–11, 5 mm long, 0.9–1.3 mm broad, narrow-linear, acute with a sharp point, glabrous, sessile, adpressed erect, not imbricate; hyaline margins serrulate and narrow; adaxially slightly concave; abaxial surface round keeled with two rows of gland dots. *Inflorescence* a terminal reduced cyme with four flowers on each outer branchlet, up to 23 flowers in a head, often much less. *Bract* one to each flower, vary considerably in size, those on branchlets smaller, about 3 mm long, 0.7 mm broad, lanceolate, acute, glabrous, apex with a sharp mucro, hyaline margins somewhat serrulate, abaxial surface convex keeled, gland-dotted. *Bracteoles* two, similar to the bract, 2 mm long, 0.6 mm broad, lanceolate, acute, mucronate, glabrous, margins ciliolate-serrulate. *Calyx lobes* five, 2.8–3.4 mm long, 1.2 mm broad, broadly lanceolate, acute, apiculate, glabrous, gland-dotted, white, hyaline margins broad somewhat serrulate sometimes ciliolate at base. *Petals* five, 3.3 mm long overall; *limb* 1.5 mm long, 0.8 mm broad, elliptic, acute, glabrous, white; *claw* 1.8 mm long, 1 mm broad, narrowing below to a short petiole-like base, strongly transversely bearded above, translucent below, margins crisped ciliate. *Staminodes* five, vestigial, a minute gland about 0.05 mm diam., between the lobes of the disc. *Filament* five, becoming 1 mm long, acicular, glabrous. *Anthers* five, before anthesis 0.9 mm long, 0.7 mm broad, wine-coloured; apical gland minute, spherical. *Pollen* 43 μ diam., obloid, narrowed at the waist. *Stigma* 0.3 mm diam., globose, capitellate. *Style* at first deflexed becoming erect, 1.5 mm long, glabrous. *Ovary* 5-carpellate, 0.8 mm diam., glabrous, apices globose. *Disc* stands open, 10 sinuate, fairly sessile, exudes nectar, very like as in *Diosma*. *Fruit* (from Williams 2209) 5-carpellate, 6 mm long, 5 mm diam., glabrous, style persisting; *carpels* shining, smooth, green below, wine-coloured, with few gland dots; horns at most 1.5 mm long, not at all cleft, sub-acute. *Seed* 4.6 long, 2 mm broad, black, shining; aril black-streaked.

Euchaetis linearis is recognised as distinct having the disc standing open as in *Diosma* and the style at some stage deflexed, having leaves linear-acute with a straight sharp point, quite glabrous, hyaline margins, serrulate or smooth and fruits with horns not more than 1.5 mm long. Another useful character is the almost petiolate shape of the petal. The numerous small gland dots in the leaves readily distinguish *E. linearis* from *E. elata* where they are much larger in size and fewer in number.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): West slopes of Swartgat Peak, Witsenberg, Tulbagh Division (-AA), 4 000 ft., 8/4/1950, *Esterhuysen 16917* (BOL); Ridge S. of Inkrui, Witsenberg Range, Ceres Division, 3 500–4 000 ft., 25/2/1973, *Esterhuysen 33143* (BOL); Little Winterhoek, N. E. side, 5 500–6 000 ft., 16/10/1960, *Esterhuysen 28528* (BOL); Great Winterhoek, 5 500 ft., 17/4/1960,

Esterhuysen 28467 (BOL); Hansiesberg, W. Slopes, Ceres Division (-AB), 3 000–4 000 ft., 18/4/1956, *Esterhuysen* 25725 (BOL); Waaihoek Plateau, Worcester Division (-AD), 5 000 ft., -/5/1942, *Stokoe* 8500 (BOL); Waaihoek Peak, 3 000 ft., 25/8/1973, *Esterhuysen* s.n. (BOL); Mostertshoek Twins, 5 000–6 000 ft., 8/1/1944, *Esterhuysen* 9818 (BOL), 9/4/1955, *Esterhuysen* 24268 (BOL); Roodeberg, Waaihoek Mountains, Worcester Division (-CB), 3 500 ft., 10/8/1952, *Esterhuysen* 20309 (BOL); Brandwacht Peak, 5 500 ft., 7/4/1963, *Esterhuysen* 30128 (BOL); Fonteintjiesberg, 5 500 ft., 6/4/1975, *Esterhuysen* 33805 (BOL), 5 000 ft., 9/3/1963, *Esterhuysen* 30075 (BOL); Villiersdorp, Caledon Division (-CD), -/11/1946, *Stokoe* 9346 (BOL).

—3418 (Simonstown): Mountain near Palmiet River Mouth, Caledon Division (-BD), -/4/1926, *Stokoe* s.n. (K, BOL 18767).

—3419 (Caledon): Pone Bot River (-AA), 1 200 ft., 27/11/1896, *Schlechter* 9454 (BM, BOL, G, GRA, K, P, PRE); In graminosis saxosis Zwartberg prope Caledon (-AB), 1 300 ft., -/7/1892, *H. Bolus* 6347 (BOL, K); Inter graminia alta (altit. IV) laterum montis Zwartberg prope thermas, Caledon -/7/-, *Ecklon & Zeyher* 820 (MEL, S); Zwartberg, Caledon -/7/-, *Zeyher* s.n. (SAM 14662); Caledon, Swartberg above the baths, 1 450 ft., 13/7/1973, *Williams* 1824 (NBG), 1 500 ft., 16/9/1976, *Williams* 2209 (NBG); Babylons Tower, Caledon Division (-AD), 23/6/1974, *Esterhuysen* s.n. (BOL); Zwartberg, Sandfontein, Caledon Division (-BA), 2 000 ft., 6/4/1897, *Schlechter* 10350 (BM, BOL, G, GRA, K, PRE).

DISTRIBUTION

Euchaetis linearis is found growing at altitudes of from 360–610 m (1 200–2 000 ft.) in the Caledon Division and further to the north in the mountains of the Worcester, Tulbagh and Ceres Divisions at altitudes of 900–1 800 m (3 000–6 000 ft.). In the Caledon Division the bracts and calyx lobes are pale, almost white in colour, while those of the populations to the north are dark or reddened. This may be due to their exposure to sunlight at higher altitudes. The total range from north to south is in the order of 130 km.

21. ***Euchaetis longicornis*** Williams in Jl S. Afr. Bot. 41 (3): 170 (1975). Type: CAPE—3421 (Riversdale): On the north slopes of Plaatjieskop between the Kaffirkuils and Soetmelks rivers (-AB). 240 m alt., 3/5/1974, *Williams* 1896 (NBG, holotype; K, MO, M, PRE, S, STE, isotypes).

Euchaetis longicornis is recognised as distinct on account of its having subulate leaves, sharply pointed bracts and bracteoles, acuminate calyx lobes and fruits with exceptionally long (7 mm) horns. In addition it should be noted that the disc stands open, exceeding the ovary.

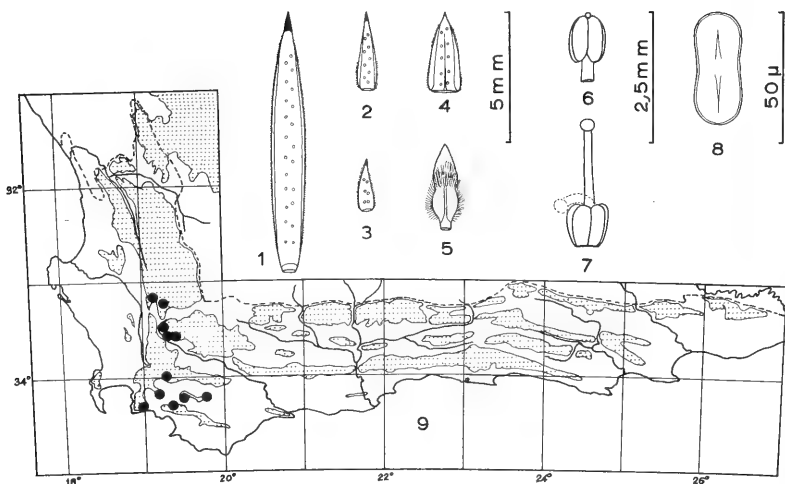


FIG. 13.

Euchaetis linearis: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, gynoecium. 8, pollen. 9, distribution.

22. *Euchaetis diosmoides* (Schltr.) Williams in JI S. Afr. Bot. **40** (4): 280 (1974).

Acmadenia diosmoides Schltr. in Bot. Jb. **24**: 439 (1898). Type: CAPE—3419 (Caledon): on sandy places near Elim, Bredasdorp Division (-DB), 100–150 m alt., 20/4/1896 *Schlechter 7654* (BOL, lectotype; BM, K, P, PRE, W).

The following description in English supplements that given in Latin by Schlechter in 1896.

Shrubs 0,3–0,4 m tall, diffuse, single-stemmed at base. *Branches* erect, slender, somewhat lax, few in number, glabrescent. *Branchlets* erect, slender, reddened, puberulous with a minute erect pubescence, well-clothed with leaves. *Leaves* 10–12 mm long, 1,5–1,7 mm broad, linear-lanceolate, acute, incurved-mucronate, dark green, indistinctly gland-dotted, petiolate, alternate; midrib fairly prominent, at first somewhat pubescent becoming glabrous; margins ciliate becoming serrulate. *Inflorescence* terminal, with up to 60 florets at the ends of very short branchlets aggregated into heads. *Bract* one to each floret, 4–4,5 mm long, 0,8 mm broad, linear-lanceolate, acute, mucronate, glabrous except for a few hairs on the prominent midrib, ciliate, obscurely gland-dotted. *Bracteoles* two, 2 mm long, 0,6 mm broad at base, lanceolate-acute, minutely mucronate, ciliolate, glabrous; margins translucent. *Calyx lobes* five, 2,6–3 mm long, 0,9–1,4 mm broad, oblong, acute, incurved-mucronate, adaxially pubescent other-

wise glabrous, brown or purplish above; margins translucent, ciliolate. *Petals* five, 4 mm long overall; *limb* 2–2.3 mm long, 1.4–1.7 mm broad, orbicular, white, subacute; *claw* 1.8–2 mm long, 0.9–1.4 mm broad, transversely bearded and ciliate above, narrowed and glabrous below. *Staminodes* five, 0.15 mm diam., vestigial, upon the elevated lobes of the disc. *Filaments* five, becoming 1 mm long, glabrous. *Anthers* five, 0.9 mm long, 0.6 mm broad, reddened, apical gland minute. *Pollen* 38 μ long, 20–25 μ broad, ellipsoid. *Disc* sinuate-crenulate, spreading, green, fleshy, exceeds the ovary at first. *Stigma* 0.3–0.5 mm diam., capitellate. *Style* 0.6 mm long, glabrous, at some stage deflexed. *Ovary* 5-carpellate, 0.7 mm diam., apices reddened. *Fruit* 5-carpellate, 4–5 mm long, 3.5–4.5 mm diam., glabrous or with a few spiky hairs along the upper edges on the inside; horns 0.7–1.0 mm long, with a sunken gland near the apex. *Seed* 2.7–2.9 mm long, 1.5 mm broad, black, shining; aril black.

Euchaetis diosmoides is recognised as distinct having the disc open, sinuate-crenulate as in *Diosma*, the style at some stage deflexed, the stigma 0.3–0.5 mm diameter, and leaves acute, incurved-mucronate. It appears to be nearest to *E. schlechteri* which differs in having the style always erect with the stigma 0.6–1.0 mm diameter.

SPECIMENS EXAMINED (additional to those previously cited)

CAPE—3419 (Caledon): 15 miles from Elim along road to Struisbaai, Bredasdorp Division (-DB), 17/9/1962, *Esterhuysen* 29689 (BOL); Toekoms near Boskloof, S. side Bredasdorp Mtns., Bredasdorp Division, 600 ft., 24/2/1977, *Williams* 2275 (NBG); S. slopes Bredasdorp Mts., 6/12/1938, *Halfstrom & Acock* 2177 (S).

— 3420 (Bredasdorp): Bredasdorp Mtns., S. end near Preekstoel Rock (-CA), 400–600 ft., 20/5/1975, *Williams* 2002 (NBG); Wild flower garden, Bredasdorp, 450 ft., 13/7/1976, *Williams* 2183 (NBG); Potberg, ridges south east of main peak (-BC), 1 000 ft., 2/1/1971, *Oliver* 3232 (STE).

23. *Euchaetis schlechteri* Schinz in Mem. Herb. Boiss. 20: 19 (1900). Type: CAPE—3418 (Simonstown): in saxosis prope Sir Lowrys Pass (-BB), 400 ft., 15/7/1892, *Schlechter* 1171 (BOL, G, GRA, K, isotypes).

The following description, done from fresh material collected near Caledon, supplements that given in Latin by Schinz.

Shrubs 250–350 mm tall, with several erect stems arising from a stoutish root-stock which may survive veld burning. *Branches* di-/tri-chotomate, slender, minutely puberulous, not hidden by the leaves, becoming glabrous and somewhat rough with leaf scars. *Leaves* varying up to 15 mm long, 2 mm broad, narrowly lanceolate, mucronate, often drawn out into a sharp point, keeled, erect spreading or recurved, alternate or opposite; margins scabrid, ciliate at first; abaxial surface and keel crisped pubescent at first becoming glabrescent,

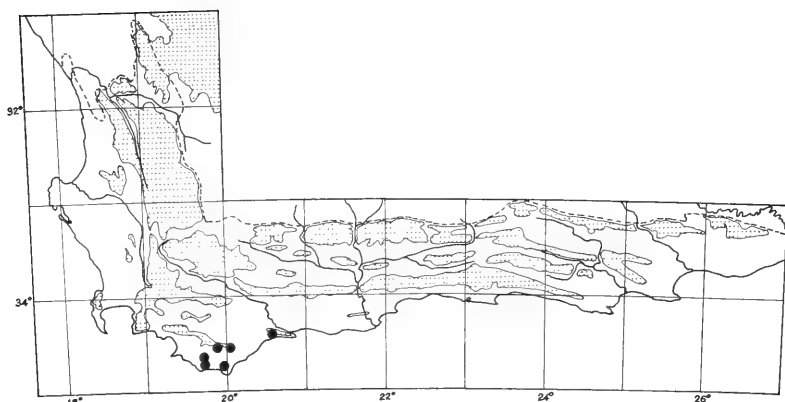


FIG. 14.

Euchaetis diosmoides: distribution.

without conspicuous gland dots; petiole very short. *Inflorescence* terminal, the flowers aggregated into compact globose heads, in groups of up to nine at the ends of up to five branchlets. *Bract* one, leaf-like, 5–7.5 mm long, 1.5 mm broad. *Bracteoles* two, 2.3–4.5 mm long, 1 mm broad, lanceolate, acute, ciliate, minutely crisped pubescent, reddened above. *Calyx lobes* five, 3–4.2 mm long, 1.6 mm broad, lanceolate, pubescent, ciliate; apex acute, purplish; margins translucent below; adaxial surface beneath the elevated purplish rib is hollowed and pubescent. *Petals* five, 4.7–5.3 mm long, white or somewhat pink; *limb* 1.5–2 mm broad, elliptic, glabrous, minutely serrulate; *claw* 1.5 mm broad, narrowing to 0.5 mm below, transversely bearded and ciliate above, one or two hairs scattered below. *Staminodes* five, 0.15 mm diam., globose, vestigial. *Filaments* five, becoming 1.5 mm long, subulate, glabrous. *Anthers* five, before anthesis 0.8 mm long, 0.7 mm broad, wine-coloured; apical gland spherical, minute. *Pollen* 53 μ long, 28 μ diam., obloid. *Disc* stands open, sinuate-crenulate, exceeding the ovary, fleshy, dark green, exudes nectar. *Stigma* 0.6–1 mm diam., capitate, dark green. *Style* becoming 1.2 mm long, glabrous, virtually always erect. *Ovary* 5-carpellate, glabrous, lobes reddened, obtuse. *Fruit* 5-carpellate, 6.3 mm long overall, almost glabrous except for a few minute hairs; horns 1.8 mm long, minutely cleft without any gland; style persisting. *Seed* 3.5 mm long, 1.8 mm broad, black, shining, the surface rippled; aril small, black.

SPECIMENS EXAMINED

CAPE—3418 (Simonstown): in saxosis prope Sir Lowrys Pass, Somerset West Division (-BB), 400 ft., 15/7/1892, *Schlechter* 1171 (BOL, G, GRA, K).

— 3419 (Caledon): clay soil above Cape Road, ¼ mile W. of Caledon (-AB), -/9/1926, *Pillans s.n.* (BOL 18567); along the National Road above Caledon on

Bot River side, 10/4/1971, *Esterhuysen* 32593 (BOL); W. end of Caledon between old road and National Road, 800 ft., 7/6/1972, *Williams* 1653 (NBG); Cape Town end of Caledon below the road, 800 ft., 13/3/1973, *Williams* 1825 (NBG); Hemel en Aarde, Caledon Division (-AC), 24/2/1941, *Esterhuysen* 5012 (BOL); clay hills E. of Bot River Bridge, 31/8/1977, *Goldblatt* 3993 (MO); Shaws Pass, Caledon Division (-AD), -/2/1940, *Walgate* 72 (BOL); N. side Shaws Pass, 8 km S. of Caledon, 285 m, 24/1/1979, *Burgers* 1707 (CPA Nature Conservation Herbarium).

— 3420 (Bredasdorp): 18 km from Bredasdorp towards Swellendam (-AC), 600 ft., 12/8/1973, *Williams* 1839 (NBG).

Euchaetis schlechteri is a distinct species most readily distinguished by the disc being open sinuate-crenulate as in *Diosma* and the capitate stigma 0.6–1.0 mm diam. The lanceolate, often pungent leaves up to 1.5 mm long, without obvious gland dots, also make it easy to recognise. It may be distinguished from *E. diosmoides* which has a much smaller stigma 0.2–0.5 mm diam.

DISTRIBUTION

E. schlechteri is found growing in clayish soil at altitudes of from 120 to 285 m above sea level in rather widely scattered localities from Sir Lowrys Pass to the Bredasdorp ruggens, but is mainly concentrated in the Caledon district. It seems to be rather rare and when found very few plants are to be seen. It may have possibly been largely eliminated by cultivation.

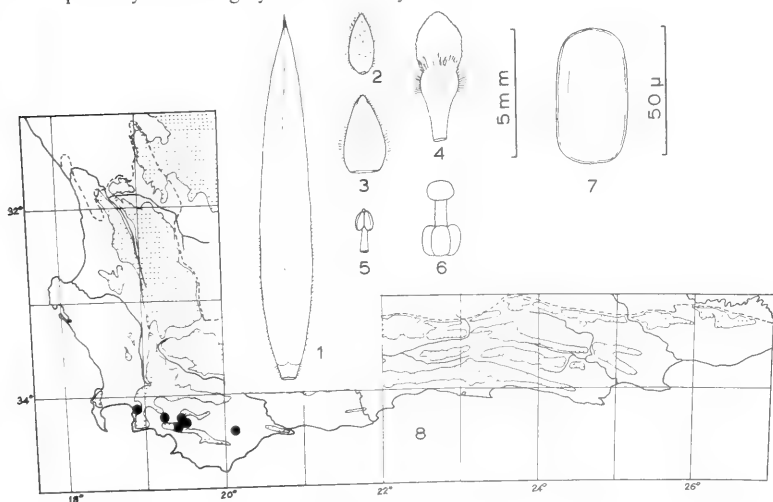


FIG. 15.

Euchaetis schlechteri: 1, leaf. 2, bracteole. 3, calyx lobe. 4, petal. 5, anther. 6, gynoecium. 7, pollen. 8, distribution.

SPECIES EXCLUDED

A. euchaetis dubia Sond. in Flor. Cap. 1: 373 (1860).

Macrostylis dubia Benth. & Hook. Gen. Plant. 1: 289 (1867).

Portions of Zeyher 291 were seen independently by both Turczaninov (1858) and Sonder (1860). As this material showed only flowers in the earlier stages before the elongation of the style and filaments had taken place Turczaninov was led to place it in *Acmadenia* and Sonder to place it, rather doubtfully, in *Euchaetis*. However it appears that this plant should rather be placed in *Macrostylis* as was noted by Bentham and Hooker (1867). Due to prior publication the epithet *cassiopoides* has precedence over *dubia* and the combination *Macrostylis cassiopoides* has therefore to be made.

***Macrostylis cassiopoides* (Turcz.) Williams, comb. nov.**

Acmadenia cassiopoides Turcz. in Bull. Soc. Imp. Nat. Mosc. 31. 1: 439 (1858). Type: Lang Valley, Zeyher 291 (S, lectotype; SAM, isotype).

B. *Euchaetis uniflora* Phillips in Ann. S. Afr. Mus, 9: 115 (1913) = *Acmadenia uniflora* (Phillips) Phillips in J1 S. Afr. Bot. 9: 137 (1943).

PHYTOGEOGRAPHY

The maps showing the distribution of species of *Euchaetis* have been combined and illustrated in Figure 2. Ten species make up a north-south distribution pattern. Here the plants are found growing in mountainous areas on quartzitic acid soils derived from the Table Mountain Sandstone. Thirteen entirely different species make up an east-west distribution pattern. Of these, three very distinct taxa are found in mountainous areas growing in acid soils derived from the Table Mountain Sandstone. A further three species are found on the coastal plain on soils associated with silcrete, ferricrete or clay and seven species are found fairly near the coast in sandy soils either on or associated with the Bredasdorp limestone beds. It should be noted that no species of *Euchaetis* is to be found on the plains of the west coast from the Cape Peninsula northwards.

Considering first the montane species which are quite distinct and well-defined, *Euchaetis tricarPELLATA* with its unique three-carpellate ovary is isolated geographically from all others being found only on Piketberg, a detached mountainous area opposite St. Helena Bay. Also, just as isolated, being the only species to be found on the whole of the Langeberg, Outeniqua and Tzitzikamma mountains, is *E. avisylvana* with its distinctive villous-ciliate leaves. Much further to the east, in the Koege and Baviaanskloof mountains, after a disjunction of about 290 km, one finds *E. vallis-simiae*, a very distinct species with the leaves gibbous behind the apex and a pubescent ovary. Still further to the east, in the Cockscomb mountains, *E. cristagalli* marks the easterly limit to the distribution of the genus.

Of the seven more or less coastal species, *E. longibracteata*, *E. laevigata* and *E. intonsa* are easily distinguished. Only the last four appear to be somewhat difficult to separate. They are *E. albertiniana*—*E. burchellii*—*E. scabriscosta*—*E. meridionalis* in that order and it is possible that hybrids between these species may be noticed in the future. The habitat they occupy is almost certainly of more recent origin than that of the montane species and it is possible that speciation here has more recently taken place. *E. burchellii* has the widest distribution of all species of *Euchaetis* being found from the Uilenkraals River in the west to Herolds Bay in the east, a distance of about 275 km.

OBSERVATIONS ON THE EFFECTS OF FIRE IN MOUNTAIN FYNBOS AT ZACHARIASHOEK, PAARL

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ABSTRACT

Changes in composition and structure of fynbos plant communities after an experimental fire in the Zachariashoek research area near Paarl, Cape Province, were assessed by means of a sample of 31 fixed 50 m² quadrats before the burn in November 1971 and again six years later.

Results show little change in vegetation between 1971 and 1977. The mean number of species per plot did not differ significantly nor did evenness or dominance concentration. Composition as measured in each plot by the relative cover-abundance of species changed by about 33% on average but when measured by species presence and absence the change amounted to some 50%. Such apparent compositional changes were however ascribed principally to misidentification of rare species and other observer errors, and local small shifts in distributional patterns, because the frequency and mean relative cover of prominent species changed little. No major changes in vegetation structure, i.e. canopy height, cover, and growth form composition, were apparent, though canopy cover seemed to decline somewhat and seed-regenerating shrubs were slightly reduced in importance.

Communities had already been subject to artificial disturbance before the burn and are therefore not likely to have represented the naturally prevalent vegetation of the area.

Thus although the vegetation largely recovered its pre-burn condition within six years this would not necessarily be the case in pristine or nearly pristine fynbos.

UITTREKSEL

WAARNEMINGS OP DIE INVLOED VAN VUUR IN BERG FYNBOS TE ZACHARIASHOEK, PAARL

Verandering in samestelling en struktuur van fynbos plantgemeenskappe in die Zachariashoek navorsingsgebied naby Paarl, Kaaprovinsie, na 'n eksperimentele brand, is vasgestel deur middel van bemonstering van 31 permanente 50 m² persele, voor die brand in November 1971 en weer ses jaar daarna.

Resultate het min verandering in die plantegroei tussen 1971 en 1977 aangetoon. Die gemiddelde aantal soorte asook die mate van gelykmatigheid, en konsentrasie van dominansie per perseel het nie beduidend verskil nie. Samestelling van elke perseel soos deur middel van relatiewe dekkinggraad gemeet, het met omtrent 33% verander, maar het met omtrent 50% verander as dit deur middel van aan- of afwesigheid van soorte gemeet word. Sulke oënskynlike verandering in samestelling kan grootliks toegeskrywe word aan verkeerde uitkenning van skaars soorte, waarnemingsfoute, en klein plaaslike veranderinge in verspreidingspatrone, aangesien die frekwensie en gemiddelde relatiewe dekking van opvallende individuele soorte min verander het. Geen noemenswaardige veranderinge in gemeenskapstruktuur, d.w.s. hoogte, dekking en groeivormsamestelling, is waargeneem nie, alhoewel kroondekking skynbaar afgeneem het en belangrikheidsgraad van generatiewe struik ietwat verlaag was.

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Gemeenskappe is voorheen kunsmatig versteur voordat dit gebrand is en het waarskynlik nie die natuurlike heersende plantegroei van die gebied verteenwoordig nie.

Dus, alhoewel die plantegroei grotendeels herstel het tot die toestand wat voor die brand geheers het, sal dit nie noodwendig die geval wees by ongeskonde of byna ongeskonde fynbos nie.

INTRODUCTION

The Zachariashoek experiment, discussed in detail by Van der Zel (1974), was established in 1965 to investigate the influence of controlled burning of Mountain Fynbos (Veld Type 69: Acocks, 1953) on water yield, erosion, and vegetation composition. The experiment includes three main experimental sub-catchments, Kasteelkloof (324,5 ha), Zachariashoek (287 ha) and Bakkerskloof (356,4 ha). Treatments consist of late spring (November) burns on six and on 12 year rotations in the Kasteelkloof and Zachariashoek sub-catchments respectively, and protection from fire in Bakkerskloof. This paper reports on change in the fynbos communities in the Kasteelkloof sub-catchment following the first prescribed treatment period.

The research area is located near Paarl in the south-western Cape Province, and is centred at 34° 49' and 19° 02' in quarter-degree square 3319CC (Fig. 1). Elevation ranges from 240 to 850 m overall but from 240 to 765 m in the Kasteelkloof sub-catchment. The only geological formation present is the Table Mountain Group, which comprises sandstones of the Peninsula and Nardouw Formations, tillites of the Pakhuis Formation, and shales and mudstones of the Cedarberg Formation (the shale band). Sandstones are the dominant parent material.

Climate is typical of mountains of the winter-rainfall zone (e.g. Schulze, 1965; Kruger, 1979). Annual rainfall in Kasteelkloof varies between 930 and 2 300 mm with a mean over eight years of 1 458 mm: further data are reported by Van der Zel (loc. cit).

VEGETATION

The dominant vegetation is a low restioid herbland, or an open low narrow-sclerophyllous shrubland, both formations dominated by coarse Restionaceae and Cyperaceae. Important genera include *Chondropetalum*, *Hypodiscus*, *Restio*, *Staberoha*, *Tetratia* and *Pentaschistis*. A sparse low sclerophyllous woodland characterised by *Protea nitida* occurs on the talus slopes along the shale band. Trees are otherwise rare. On rocky koppies stunted broad-sclerophyllous trees, mainly *Heeria argentea*, form a closed scrub while in ravines stunted forest of mainly sclerophyllous trees may be found. A detailed report on the vegetation of Zachariashoek is in preparation.

HISTORY OF THE CATCHMENTS

The upper portion of the catchment has always been unoccupied state land.

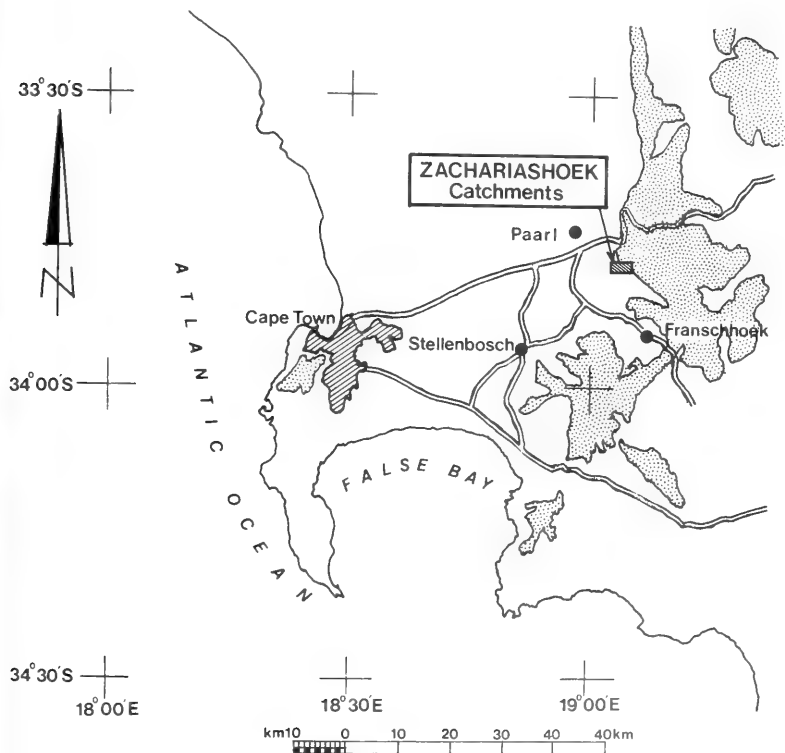


FIG. 1.

Location of the Zachariashoek catchments. Shaded areas represent land at elevations above about 600 m.

The lower portion was granted as freehold in 1839, but transferred to the Department of Forestry in 1940.

There is no record of grazing in the area, but land in private ownership would very likely have been used at a low intensity for seasonal rough pasturage of large and small stock, and this would have been associated with irregular but frequent burning (see, for example, Wicht and Kruger, 1973). Areas of state-owned land would also most likely have been similarly used on a casual basis. Irregular tracks, bare areas and gullies encountered in the catchments are apparent testimony of use by domestic stock. It is unlikely that pasturage was of any real consequence during the past quarter century, and it has certainly been minimal since 1965.

The recent history of fire in the area is fairly well documented, but no records of fires predating 1953 could be found. The entire area appears to have burnt out in two fires in 1953 and 1954, as reflected in the following reports: "The Du Toits Kloof fire raged on the Wemmershoek Mountains from 6–10th March 1953 destroying part of the veld on the Zachariashoek Reserve, the whole of the Wemmershoek Reservoir Area and part of the Wemmershoek Catchment area" (Annual Report of the Conservator of Forests, 1952–53: Department of Forestry files); "A fire started on the City Council land at Wemmershoek or Zachariashoek Forest Reserve (in March 1954), destroying all the veld saved from the fire that ravaged the Klein Drakenstein Mountains during March 1953" (Annual Report of the Conservator of Forests, 1953–54: Department of Forestry files).

TABLE 1.
Fire history of the Zachariashoek catchments

Date of fire	Percentage of sub-catchment area burnt			Cause of fire or reason for burning
	Kasteelkloof	Bakkerskloof	Zachariashoek	
1953–54	100,0	100,0	100,0	Unknown
1960	2,1	31,9	27,1	Unknown
1963	23,8	0,4	0,0	Site preparation for planting
1965	67,4	51,8	12,3	Hakea control
April 1966	0,0	0,0	31,5	Unknown, possibly Hakea control
Aug. 1966	0,0	0,0	14,9	Firebreak
Aug. 1969	3,6	11,6	0,0	Hakea control
Aug. 1970	0,0	0,0	±1,0	S.A. Air Force flare
Aug. 1971	0,0	3,0	10,0	Firebreak
Nov. 1971	100,0	0,0	0,0	Prescribed burn
Sept. 1972	0,0	10,6	0,0	Firebreak
Aug. 1973	0,0	0,0	6,7	Firebreak
Nov. 1977	100,0	0,0	100,0	Prescribed burns

The subsequent fire history for the entire catchment experiment, as obtained from Departmental reports, aerial photographs, and ground observation, is presented in Table 1.

Much of the area, and especially Kasteelkloof, was densely infested by *Hakea sericea* Schrad. and scattered large *Pinus pinaster* Ait. trees before 1965 (J. A. Fenn, 1978, pers. comm.). These woody weeds were cut down by hand and the seed was allowed to germinate before the burn prescribed for 1965. These measures were repeated before the 1971 burn in Kasteelkloof and ensured nearly complete eradication of the weed populations.

Before the decision in 1965 to use the area for research it had been earmarked for timber plantations. The lower portions of Zachariashoek and Kasteelkloof were afforested with *Pinus radiata* D. Don during 1963–64. Site preparation included burning and pitting. The pines were later killed by fire or removed by hand during operations in 1965 and 1971.

Although human influences and fire have pervaded the experimental area their impact has been limited, often being difficult to discern or otherwise local. Implications regarding experimental results are discussed below.

METHODS

A set of 33 permanent quadrats, each 50 m² (5 × 10 m) in area, was established to monitor community composition. Each plot was located on the intersection of a 300 m grid (orientated N-S and E-W) in the Kasteelkloof catchment, and each was marked by means of a creosoted wooden pole planted at a standard bearing and distance from the plot corner.

Each plot was defined by means of braided nylon cords, staked carefully to ensure a rectangular shape. Plots were quartered with shorter cords, to aid cover-abundance estimates.

The vegetation in each plot was analysed in September to October of 1971. All vascular plants in the plot were listed and classified by cover-abundance estimates on the Braun-Blanquet scale, as described by Kuchler (1967). Unidentifiable herbs were listed as such. Species seen in a belt approximately 2 m wide surrounding the plot were also noted, but the surrounds were not searched thoroughly. All but one of the plots were relocated in the spring (September to October) of 1977, and the same procedure followed. One plot did not burn in 1971, and this unit was discarded from our sample. Geophytes and other species which could not be recognized throughout the year were deleted from the data before any analysis.

Field surveys had been preceded by botanical collections so that a reasonable reference herbarium was available; the flora was in any case relatively well known to one of us (F.J.K.). Specimens were collected from species which could not be identified in the field and these were assigned a serial number until positive identification was possible.

One of us (F.J.K.) completed all enumerations during 1971, and participated in much of the field work during 1977. Cover-abundance estimates and field identifications were co-ordinated during joint field excursions. Identification of problematic plant specimens was undertaken jointly in the herbarium.

Total vegetation cover on each plot was estimated in 1971 but not in 1977 because it was thought that these estimates would be too inaccurate to demonstrate small changes in cover. This was unfortunate, because the estimates would have served to indicate large changes (see below). Also, height and cover of vegetation strata were recorded in 1971 but not in 1977. A more exact technique

was adopted in which we recorded heights of an arbitrary sample (not random) of 10 individuals of each prominent species in each plot. Most sites were photographed before and after each burn and these photographs aided later interpretation of results.

Species' mode of post-fire regeneration was determined by observation in the field (species which resprout are easily identified: Martin 1966) or knowledge of their behaviour elsewhere (Van der Merwe, 1966).

RESULTS

Growth forms

All species present in the survey were classified into growth forms, as follows: Trees, shrubs (>1 m in height), low shrubs (between 0.25 and 1 m), dwarf shrubs (less than 0.25 m), Restionaceae, Cyperaceae, Poaceae, and other herbs including ferns. Members of each of these were classified according to mode of regeneration after fire as vegetative (v), germinative (g—regenerating from seed only), or unknown (u).

TABLE 2.
Summary of changes in growth-form composition (see text).

Growth forms	Mode of re-generation	Mean canopy cover, %		Frequency %	
		1971	1977	1971	1977
Trees	v	0.07	0.05	3	3
	g	0.02	0.00	2	0
	u	0.00	0.00	0	0
Shrubs (> 1 m)	v	6.9	10.1	17	18
	g	8.7	4.1	29	29
	u	0.12	1.3	8	7
Low shrubs (0.25 – 1 m)	v	6.0	4.4	29	29
	g	17.7	15.7	30	30
	u	2.4	2.1	21	19
Dwarf shrubs (< 0.25 m)	v	1.0	1.1	26	23
	g	0.66	0.66	20	23
	u	0.17	0.65	8	5
Restionaceae	v	45.1	34.3	31	31
	g	0.00	0.00	0	0
	u	0.00	0.00	0	0
Cyperaceae	v	15.0	8.2	31	30
	g	0.00	0.00	1	0
	u	0.00	0.00	0	0
Poaceae	v	12.1	11.0	29	30
	g	0.08	0.08	6	5
	u	0.00	0.00	0	0
Others	v	5.8	10.6	30	30
	g	0.36	0.44	16	20
	u	0.89	2.2	15	30

Percentage cover values for each species record were assigned to the cover-abundance scale as follows: r = 0,1; + = 0,5; 1 = 3; 2 = 15; 3 = 37,5; 4 = 62,5 and 5 = 87,5 %. Values were accumulated for all species in each growth form in each plot to calculate means for the sample. Data appear in Table 2.

Total cover

A rough estimate of the cover in each plot was obtained by calculating the sum of cover values for each species using the scale conversion presented above. Results appear in Table 3.

TABLE 3.
Comparison of calculated cover values in each plot for both surveys
(see text for explanation)

Plot number	Cover, %		Plot number	Cover, %	
	1971	1977		1971	1977
21	70	65	38	104	84
22	182	142	39	85	87
23	107	170	40	124	94
24	152	190	41	85	94
25	97	73	42	98	57
26	169	127	43	88	78
28	136	139	44	187	166
29	129	146	51	103	100
30	188	175	57	86	100
31	141	120	58	84	54
32	163	57	59	184	163
33	175	72	60	108	111
34	77	50	73	127	145
35	77	65	74	107	99
36	105	59	75	177	165
37	101	60	Mean	120	107

Diversity

Measures of species diversity are presented in Table 4. Simpson's index—a measure of dominance concentration—was calculated for each plot as $C = \sum^s p_i^2$ where s = the number of species in the sample and p_i = the proportional abundance of the i th species (see Whittaker, 1972). The Shannon-Wiener index, which reflects evenness of relative species' abundances in the community, was calculated as $H = - \sum^s p_i \log_{10} p_i$ (Whittaker, 1972).

Height

Grand mean heights for each species measured were calculated from the 1977 data as well as means for each species in each plot. In this manner mean heights for almost all important species occurring in the catchment were obtained. Comparison with estimates for each stratum made during 1971 showed little evident change in the height and stratification. This is supported by examination of photographs of each site (Figs 2 to 7).



FIG. 2.
Plot No. 25 before the burn in 1971.



FIG. 3.
Plot No. 25 in 1977. Note survival and recovery of *Heeria argentea* (extreme left and right) and *Widdringtonia nodiflora* (centre).



FIG. 4.
Plot No. 30 before the burn in 1971.



FIG. 5.
Plot No. 30 in 1977. *Pinus radiata* has been killed by fire or removed subsequently. Shrub with pale inflorescences is *Serruria rosea*. Riparian scrub along stream in background has not returned to 1971 stature, but had apparently been protected against fire for some time before 1971.



FIG. 6.
Plot No. 43 in 1971.



FIG. 7.
Plot No. 43 in 1977. Note depletion of *Leucadendron microcephalum* along drainage line in background.

TABLE 4.
Species diversity data for both surveys
(see explanation in text)

	1971	1977
Number of species in sample	260	267
Mean per plot	39,7	38,9
Standard deviation	10,3	9,9
Maximum per plot	55	57
Minimum per plot	6	7
Number common to both surveys	220	220
Mean Simpson's Index	0,05	0,05
Standard deviation	0,05	0,04
Mean Shannon-Wiener Index	1,45	1,49
Standard deviation	0,20	0,19

Cluster analysis

Relative change in species composition of the vegetation was assessed by means of cluster analysis. Records of botanical composition for each plot in both the 1971 and 1977 surveys were treated as a single data set. The results of a cluster analysis using the Bray and Curtis measure of similarity (Bray and Curtis, 1957), are depicted in Figure 8. A summary of the similarity analysis is presented in Table 5. For this analysis, cover-abundance values were scaled as follows: r = 1, + = 5, 1 = 10, 2 = 20, 3 = 30, 4 = 40, and 5 = 50.

TABLE 5.
Summary of similarity analysis

Number of plots	31
Mean similarity (%)	67,2
Standard deviation	6,7
Minimum similarity (%)	49,4
Maximum similarity (%)	77,5
Mean similarity for most similar pairs of plots	37,1
Standard deviation	10,7

Changes in relative abundance of species

Mean cover per species, calculated as for life forms, and frequency in both surveys are presented in Table 6 (less important species are omitted).

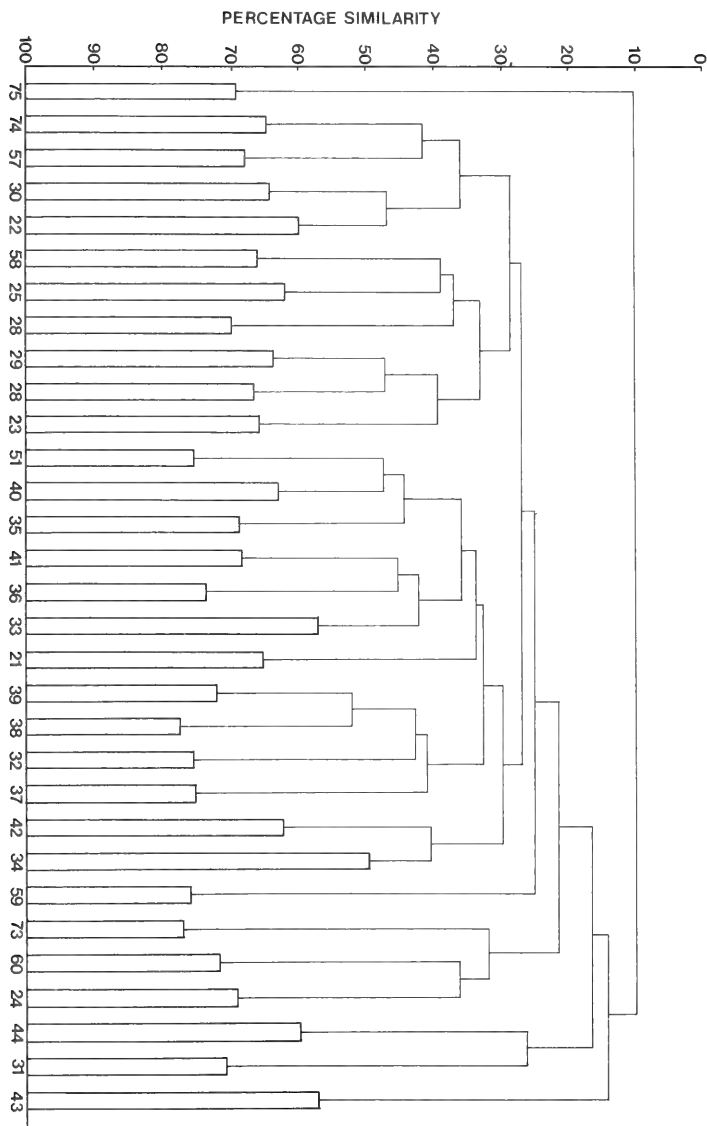


FIG. 8.

Dendrogram for the cluster analysis of permanent plot records (see text). The lowest branches (highest similarity) represent degree of similarity between successive records on each plot, and the next lowest, the degree of similarity between pooled records of most similar pairs or larger sets of plots.

TABLE 6.

Calculated cover percentage and frequency of common plant species in Kasteelkloof

Family	Species	Mean cover %		Frequency (number of plots)	
		1971	1977	1971	1977
Restionaceae	<i>Restio filiformis</i> Poir.	8,1	7,6	22	21
	<i>R. gaudichaudianus</i> Kunth	7,6	7,9	14	13
	<i>Chondropetalum paniculatum</i> Pillans	7,2	6,3	17	15
	<i>Staberoha cernua</i> (L.f.) Dur. et Schinz	6,6	6,1	18	17
	<i>Hypodiscus argenteus</i> Mast.	6,2	5,4	16	15
	<i>Restio cuspidatus</i> Thunb.	4,1	4,0	18	19
	<i>Thamnochortus dichotomus</i> (Rottb.) R. Br.	5,2	3,4	16	16
	<i>Leptocarpus distichus</i> Pillans	2,9	1,6	16	10
	<i>Hypodiscus aristatus</i> (Thunb.) Nees	2,6	2,4	10	10
	<i>Restio triticeus</i> Rottb.	2,6	3,1	11	15
	<i>Pentaschistis colorata</i> (Steud.) Stapf	8,3	8,7	19	19
	<i>P. curvifolia</i> (Schrad.) Stapf	2,3	2,3	11	12
	<i>Themeda triandra</i> Forsk.	2,6	1,9	3	3
	<i>Cymbopogon marginatus</i> (Steud.) Stapf	1,0	0,7	6	4
Cyperaceae	<i>Merxmuellera rufa</i> (Nees) Conert	2,6	4,2	15	20
	<i>Tetraria ustulata</i> (L.) C.B. Cl.	5,8	5,0	13	17
	<i>Tetraria cuspidata</i> (Rottb.) C.B. Cl.	5,0	5,7	23	22
	<i>Ficinia fliformis</i> (Lam.) Schrad.	3,7	2,9	22	18
	<i>Tetraria involucreata</i> (Rottb.) C.B. Cl.	3,6	2,8	10	8
Ericaceae	<i>Erica taxifolia</i> Ait.	3,4	2,1	9	8
	<i>E. hispidula</i> L.	3,0	1,8	17	10
	<i>E. plukenetii</i> L.	2,8	1,8	15	11
	<i>E. grandiflora</i> L.f.	1,8	1,3	7	6
	<i>E. coccinea</i> L.	0,9	1,1	8	7
	<i>Erica nudiflora</i> L.	1,7	0,7	6	4
	<i>E. walkerii</i> Andr.	0,8	0,3	4	2
	<i>E. imbricata</i> L.	0,4	0,2	3	1
	<i>Phyllipia leucana</i> Klotsch	1,0	0,7	5	3
	<i>Sympieza articulata</i> (Thunb.) N.E. Br.	0,8	0,8	3	2
Proteaceae	<i>Serruria subsericea</i> Hutch.	1,9	1,7	4	5
	<i>Serruria rosea</i> Phillips	0,7	0,3	1	1
	<i>Leucadendron salignum</i> Berg.	1,5	1,8	6	5
	<i>L. spissifolium</i> (Salisb. ex Knight) I. Williams	1,5	1,8	5	5
	<i>Protea nitida</i> Mill.	0,9	1,1	4	4
Asteraceae	<i>P. acaulos</i> (L.) Reichard	1,0	1,1	6	5
	<i>Ursinia crithmoides</i> (Berg.) Poir.	3,7	2,7	21	18
	<i>Elytropappus glandulosus</i> Less.	5,8	8,1	20	19
	<i>Stoebe plumosa</i> Thunb.	3,4	2,7	19	14
	<i>Corymbium glabrum</i> L.	5,0	6,6	23	25
	<i>Metalasia muricata</i> (L.) R. Br.	3,3	1,9	14	9
	<i>Euryops abrotanifolius</i> (L.) DC	2,5	1,6	5	7
	<i>Corymbium scabrum</i> L.	1,5	1,8	9	11
	<i>Cliffortia ruscifolia</i> L.	3,9	1,8	10	9
Others	<i>Anthospermum aethiopicum</i> L.	3,0	3,1	8	7
	<i>Montinia caryophyllacea</i> Thunb.	3,4	3,7	9	9
	<i>Anthospermum ciliare</i> L.	2,9	3,0	17	19
	<i>Heeria argentea</i> (E. Mey.) O. Kuntze	1,6	2,4	5	5
	<i>Widdringtonia nodiflora</i> L. Powrie	1,1	1,3	3	4
	<i>Maytenus oleoides</i> (Lam.) Loes.	0,5	0,5	4	3

Species turnover

Changes in the number of species are summarised in Table 7. Losses refer to species which occurred in a relevé in the first survey but not in the second survey. Additions are the opposite.

TABLE 7.
Species turnover observed in Kasteelkloof plots
(see text for explanation)

	Losses	Additions
Total over all plots	336	314
Number of species involved	171	149
Net change in species	40	47
Mean per plot	10,13	10,87
Minimum per plot	2	1
Maximum per plot	17	26
No. of sp-records with cover-abundance value		
r	103	26
+	211	267
1	18	17
2	4	4

DISCUSSION

Plant community structure

Relative importance of growth forms as summarised in Table 2 shows that there has been little overall change in plant community structure. Any differences that do occur are generally too small to be considered significant. The disappearance of seed-regenerating trees is due to the removal of pines, and does not reflect any change in the natural vegetation.

Most estimates of cover were lower in 1977 than in 1971 (22 lower, 9 higher: Table 3). Canopy cover appears not to have recovered fully in the six years after the fire. However, the major changes in cover indicated, for example, in the cases of plots 23 and 32 are probably due partly to observer error, exaggerated by the method used here to scale cover-abundance categories for our calculations. Inspection of successive photographs did not indicate such large changes in cover at any plot.

Plant species diversity measures changed little. The mean number of species per plot remained nearly the same. Of 260 species recorded in 1971 and 267 recorded in 1977, 220 were common to both surveys. Of the 40 species which disappeared after 1971, 29 occurred only once and 7 occurred only twice. Fifteen of these were not positively identified and two were pine species. Of 47 species which were added in 1977, 27 occurred only once and 8 occurred only twice. Ten of these were not positively identified, and a number may have been misidentified. Thus these changes are due in some measure to observer error.

Botanical composition

Percentage similarity, as summarised in Table 5, indicates the degree of compositional change which has taken place in each plot. Although some change has taken place in each plot (i.e. no plot is 100 % similar to what it was six years before) composition of the stand in each plot resembled that of the pre-burn stand more closely than any other stand. In fact the average percentage similarity between the pairs of successive records is much greater than the average between different but most similar pairs of plots (Fig. 8).

Changes in mean cover and frequency for some common species are summarised in Table 6. The Restionaceae, Poaceae and Cyperaceae, which are almost exclusively vegetative in mode of regeneration following fire, show little change.

On the other hand the Ericaceae, which rely for regeneration on seed reproduction, show a general reduction in both cover and frequency although they have by no means disappeared. Proteaceae, Asteraceae and some other taxa showed little change.

The species turnover recorded in Table 7 is not as marked as it seems. One hundred and three losses were represented by records of species with cover abundance values of r (i.e. represented in a given plot by a single small individual or shoot), and 211 by records with values of +. Additions were records mainly with values of + (267) though some had values of r (26).

On re-inspection of the field data and certain sites in the field, it became obvious that some additions or losses are due to misidentification, or incomplete identification of species, or to species being overlooked. It seemed that all or nearly all additions or losses in the cover-abundance category 2 can be attributed to misidentification. For instance *Tetraria flexuosa* (Thunb.) C.B.Cl. with a cover-abundance value of 2 in plot 34 disappeared but *Tetraria ustulata* was added to the list with a cover of 2; these two species may be confused when in the vegetative state. Some species "lost" from a plot were found in the surround, and some additions to the plot were previously found in the surround. Thus, some turnover is real, but much is spurious, due to sample and observer error. Apparent turnover is in any event confined mainly to rare species, while frequency and relative cover of more important species showed little change (cf. Table 6).

CONCLUSION

This study clearly illustrates the difficulties facing the field ecologist who studies plant communities in the fynbos, in that species' identification is a real problem even for those with experience. Where 60 or more species are enumerated in a sample unit the task merely of compiling the list without inadvertently omitting or misnaming a species is a major one, the more so when work schedules require fairly rapid sampling. This problem is compounded by the fact that

the taxonomic status of many species is poor, and this is especially so of important Cape families such as Cyperaceae and Restionaceae.

The method of monitoring vegetation as applied here was designed to detect only major trends and not for subtle changes over shorter periods of time. The rugged terrain renders intensive sampling impracticable, and precludes any quantitative estimate of important community parameters such as biomass and cover, for the whole catchment. Rare species (not included in Table 6) proved of little value as indicators of trend, and can be used only with the greatest caution. Useful ecological data will accumulate from repeated assessments of the sample, but their value must be increased through improved field identification of plant specimens, and more effective field procedures in general. Our experience with this sample has shown clearly that observers should work in pairs, not only to reduce fatigue by alternating roles of observer and recorder, but also to search jointly and so reduce the likelihood of overlooking or misidentifying species (Preston, 1979). It is plainly a false economy to work alone.

In spite of the relatively imprecise data from our samples we conclude that there has been little change in the plant communities in Kasteelkloof from their condition before the burn of 1971 to that before the 1977 burn, except that canopy cover apparently declined. Height, species diversity, species composition, and life-form composition returned essentially to pre-burn levels, with a few important exceptions. Post-fire succession is apparently of the "autosuccessional" type, where the initial floristic composition of the regenerating stand is very like that of the pre-burn stand and in turn determines composition of the developed stand (Hanes, 1971; Kruger, 1979). However, there appears to have been a meaningful reduction in the incidence and importance of certain shrubs which survive fire only through seed regeneration (e.g. Table 6: *Erica hispidula* and *E. plukenetii*). Field observations and comparison of photographic records indicate reduced abundance of other seed-regenerating shrubs, such as *Leicadendron microcephalum* Gandoger (see Fig. 17).

Changes in these communities (or the apparent lack of change) must be interpreted in relation to the history of the catchment. Most of the vegetation was burnt at 9–11 years' age in 1963 and 1965, and was therefore six to eight years old when the first experimental burn was applied in 1971. Furthermore, gully erosion in parts and tentative signs of grazing suggest significant deflective influences in the first half of the century. In consequence, the vegetation when sampled in 1971 is likely to have been altered from a natural condition. For example, *Protea laurifolia* Thunb., though fairly abundant as large, mature shrubs along the rocky scarp that runs through the area, occurred elsewhere mainly as scattered juvenile plants. We have seen that *P. laurifolia* is a species whose individuals tolerate a fairly intense fire but does not regenerate vegetatively if scorched off. Youth periods are rather long, and population maintenance depends on reasonable rates of survival rather than on rapid development

to maturity between fires; thus, when adults of a sub-population are depleted local extinction may become likely. It seems that past influences in Kasteelkloof had depleted *P. laurifolia*, which probably dominated many communities previously. The combined effects of *Hakea* encroachment, and the subsequent eradication operations, could have been responsible for this.

Hakea stands were extremely dense, like the notorious concentrations in the adjoining Wemmershoek catchment (i.e. more than about 100 individuals per ha—J. A. Fenn, 1978, pers. comm.), and this is born out by the abundance of old follicles and partly burnt stems which litter the ground over much of the catchment. These dense stands should have suppressed the natural vegetation to a large extent. The subsequent control treatment, which consists of felling the *Hakea* and burning the veld 12 to 24 months afterwards, would have resulted in further suppression of the vegetation (by the mass of reclining stems), and the hot fire would have had a marked impact on regeneration and subsequent community structure.

The net effect of this and other influences in the catchment would be expressed as (1) relative poverty of shrub life forms in the vegetation, (2) relatively low canopy cover and (3) relatively low strata, compared with the natural communities normally to be encountered in such areas. This is confirmed by field observation, and reflected in the photographs. The relatively short interval between fires should also tend to reduce the incidence of shrub species which rely on seed for regeneration (Jordaan, 1949).

Consequently, the effect of the experimental burning régime would be less than is likely to have been the case if the vegetation were in a pristine condition. Recovery to the pre-burn condition was relatively rapid because species that develop slowly have already been depleted. It is therefore not permissible to argue from our results that fynbos communities in general will not change if subject to regular fire at the relatively short interval of six years. Our and others' observations of vegetation subjected to short rotation fire régimes elsewhere show the opposite.

Nevertheless, the impact of the experimental régime is in some respects less than may have been predicted from present hypotheses, which suggest that fynbos plant species are vulnerable to short rotation burns (Jordaan, loc. cit.). Many seed-regenerating shrubs survived the 1971 burn (see Table 7; many others such as *Serruria rosea*, were observed in the field), and this agrees with observations (Kruger, 1979) that though there is considerable variation in the demography of such species, many mature fairly quickly. It is probable, however, that the six-year burning rotation would steadily deplete seed-regenerating shrub populations because the stock of seed in the populations is not allowed to grow to optimum levels. As the experiment progresses this postulation may be tested rigorously by comparison with response of vegetation to 12-year burns in Zachariashoek sub-catchment.

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A FLORISTIC DESCRIPTION AND STRUCTURAL ANALYSIS OF THE PLANT COMMUNITIES OF THE PUNDA MILIA—PAFURI—WAMBIYA AREA IN THE KRUGER NATIONAL PARK, REPUBLIC OF SOUTH AFRICA:

1. THE HYGROPHILOUS COMMUNITIES

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ABSTRACT

The topography, drainage, geology, soils, climate and biotic factors of the study area, situated in the northern part of the Kruger National Park, are discussed. The floristic classification of the vegetation was done by means of the Braun-Blanquet method whereas the Variable Quadrant Plot method was used for the structural analysis. The vegetation was divided into three main groups, namely the Hygrophilous, the Sandveld and the *Colophospermum mopane* communities. A floristic description of the Hygrophilous communities is included in this paper.

UITTREKSEL

'N FLORISTIESE BESKRYWING EN STRUKTURELE ANALISE VAN DIE PLANTGEMEENSAPPE VAN DIE PUNDA MILIA—PAFURI—WAMBIYA GEBIED IN DIE NASIONALE KRUGERWILDTUIN, REPUBLIEK VAN SUID-AFRIKA: 1. DIE HIGROFILIESE GEMEENSAPPE

Die topografie, dreinerings, geologie, grond, klimaat en biotiese faktore van die studiegebied, wat in die noordelike gedeelte van die Nasionale Krugerwildtuin geleë is, word bespreek. 'n Floristiese plantegroei-klassifikasie is met behulp van die Braun-Blanquetmetode daargestel, terwyl die strukturele analise met behulp van die Varieerbare Kwadrantperseelmethode gedoen is. Die plantegroei is in drie hoofgroepe ingedeel, naamlik die Higrofiliese-, Sandveld- en *Colophospermum mopane*-gemeenskappe. 'n Floristiese beskrywing van die Higrofiliese gemeenskappe word in hierdie artikel gegee.

INTRODUCTION

It is a well-established fact that nature reserves have to be managed and Edwards (1976) states that: "The kind and degree of control necessary, depends on the three main purposes of nature reserves: to conserve species and ecosystems; to preserve the natural aesthetic character of the landscape; and to satisfy certain needs of what may broadly be termed the public."

*Based on an M.Sc. thesis, University of Pretoria.

The Kruger National Park was created primarily to conserve the animal and plant life of the area (Van der Schijff, 1957). The conservation of the animal life in an area is impossible without the conservation of the area's plant life. To achieve this aim sound conservation and management policies are essential (Edwards, 1972). These must be based on a thorough knowledge of the ecosystem which should include a detailed classification of the vegetation of the area.

According to Van Wyk (1972) the first records of plants collected in the Kruger National Park date back to the previous century. Herbert Lang collected approximately 300 species during 1932, while C. Letty and A. A. Obermeyer also collected plants during the 1930's. In more recent years plant collections and/or descriptions of the vegetation of the northern part of the Kruger National Park have been made by Codd (1951), Acocks (1975), Van der Schijff (1957, 1969), Brynard (1961), Van Wyk (1971, 1972, 1974) and Werger and Coetzee (1977).

The necessity of a floristic-structural classification of the vegetation in the Kruger National Park has however only gained importance in the past few years because it has now become increasingly evident that such information can contribute to the formulation of sound conservation and management programmes. The main object of this study therefore was to provide a floristic-structural classification and description of the woody vegetation of the Punda Milia-Pafuri-Wambya area and where possible to correlate the vegetation types with environmental factors. The results are recorded in a series of three papers of which this is the first.

STUDY AREA

Location

The study area is situated in the Kruger National Park between $22^{\circ} 20'$ and $22^{\circ} 45'$ latitude and $30^{\circ} 55'$ and $31^{\circ} 25'$ longitude and is bordered by Zimbabwe to the north and by Mozambique to the east (Fig. 1). The area is divided into the following regions:

- (a) the Punda Milia area, which is situated north of $22^{\circ} 45'$ latitude, up to the Levubu River in the north and west of the tarred road between Punda Milia and Pafuri;
- (b) the Pafuri area, which includes the land between the Levubu and Limpopo Rivers and south to the Caborra Bassa-Apollo power lines, east of the tarred road; and
- (c) the Wambya area, from the $22^{\circ} 45'$ latitude to the Caborra Bassa-Apollo power lines in the north, east of the tarred road.

The study area covers approximately $1\,586\text{ km}^2$. The longest distance in a north-south direction is almost 46 km, whereas the longest distance in an east-west direction is approximately 53 km.



FIG. 1.
Location of the Punda Milia—Pafuri—Wambiya area in the Kruger National Park

Topography

The study area lies between 197 and 643 m above sea level and includes mountains, hills and plains. The prominent hills around Punda Milia form part of the eastern foothills of the Soutpansberg mountain range. A number of valleys which run from east to west, occur between the hills to the west and north of Punda Milia. The rivers and streams in these valleys all flow towards the Levubu River which forms the western border of the study area. On its way to the Limpopo River, the Levubu has carved a deep gorge through the Waterberg Sandstone as well as the Cave Sandstone Formations. In some places the cliffs on either side of the Levubu River reach 185 m in height and are especially striking at Lanner Gorge west of Pafuri. Schutte (1974) described the areas underlain by Cave Sandstone of the Karroo System, as among the most picturesque in the Kruger National Park. From Xantangelane northwards, the Cave Sandstone appears typically as outcrops or as inselbergs on basalt plains, although the basalt is stratigraphically higher than the Cave Sandstone.

The areas underlain by shale and basalt (Fig. 2), are generally flat or undulating and the landscape is dominated by *Colophospermum mopane* shrubs. Between the Levubu and Limpopo Rivers however, the basalt forms prominent northwest-southeast running hills.



FIG. 2.

Geological map of the Punda Milia—Pafuri—Wambya area in the Kruger National Park (Drawn after Schutte, 1974).

LEGEND

1:490 000 (approx.)

	ALLUVIUM								
	SOIL								
	LIGHT RED AND WHITE SAND								
	GRAVEL, SOIL								
	CONGLOMERATE, MERREL, FLESH COLOURED TO WHITE SANDSTONE								
	DOLORITE (DYKES, SILLS)								
	BASALT, LIMBURGITE								
	FINELY TEXTURED SANDSTONE								
	MUDSTONE, CHERT								
	SHALE WITH COAL SEAMS, MUDSTONE AND GRIT DEPOSITS								
	DIABASE								
	DIABASE OR DOLORITE DYKE (MINOR FAULT)								
	SANDSTONE, QUARTZITE WITH INTERBEDDED ANDESITE								
	ANDESITE WITH TUFF, INTERBEDDED SANDSTONE AND QUARTZITE								
	FAULT								
	ESCARP								
	POWER LINE								
	INTERNATIONAL BORDER								

QUATERNARY

CRETACEOUS
?

POST
KARROO
INTRUSIONS

STORMBERG

SERIES

KARROO
SYSTEM

ECCA
SERIES

POST
WATERBERG
INTRUSIONS

WATERBERG
SYSTEM

The Malvernian Formation at Malonga on the eastern border forms two plateaus on either side of the Shilaladonga stream. Due to a strong run-off from the plateaus to the donga, this area is severely eroded. On the plateaus themselves drainage is poor and a large number of pans occur. The sandy plateau at Shirombe has an altitude of 520 m above sea level while the basalt plains west of Shirombe are situated approximately 400 m above sea level. Broad flood plains are found along some of the streams and they are especially well developed along the Limpopo and Levubu Rivers.

Drainage

The study area is drained mainly by the Limpopo and Levubu Rivers and their tributaries such as the Madzaringwe, as well as a number of streams such as the Shilahlandonga, Shisha and Hlamalala. The most important perennial fountains are at Shipudza, Matukwale, Malonga, Tshalungwa and Kloppefontein. In the southern part of the study area along the Hlamalala, Shisha and Nwashitsombe streams, dambos are found where, due to poor drainage, waterlogged conditions often exist.

Geology and Soils

The discussion of the geology of the study area (Fig. 2) is based on the description by Schutte (1974). In the vicinity of Punda Milia a period of intense andesitic vulcanism was followed by the deposition of sedimentary rock (sandstone and shale). At a later stage sills and dykes were formed in the rock of the Waterberg System by the intrusion of diabase. Sandstone, quartzite, underlying conglomerate and shale occur as outcrops from the Punda Milia Gate in the south to Madzaringwe in the north. The prominent hills near Punda Milia, e.g. Gumbandebvu, Thula Mila and Shitshova consist of sedimentary rock (Schutte, 1974). In the study area the Karroo System is present as

- (a) basalt; and sandstone of the Cave Sandstone Stage,
- (b) mud stone of the Red Beds Stage and
- (c) shale of the Eccia Serie.

The Eccia Serie consists of shale in which deposits of coal, mud stone and grit stone occur. This Serie forms outcrops from Madzaringwe in the north to Dzundwini and beyond in the south. Rocky outcrops of the Cave Sandstone Stage appear from the Limpopo southwards to beyond Xantangelane. Basalt and limburgite of the Drakensberg Stage occur as a broad strip which is bordered on the west by Cave Sandstone. In the east it is fringed by the Malvernian Formation and more recent sand deposits. The basalt stretches from the Limpopo River southwards to Shingwidzi.

The Malvernian Formation consists of conglomerate, calcareous sandstone, merrel and consolidated gravel (Keyser, 1972; Schutte, 1972, 1974). The

sedimentary rock of the Malvernian Formation has been eroded by the Limpopo and Levubu Rivers at two localities within the study area, namely at Matulekop and Shilahlandonga and at Malvernian in southeastern Zimbabwe (Cox, 1963).

The Wambiya area on both sides of the Shilahlandonga is characterised by flesh coloured to white sandstone and aeolian sand that were deposited on the Malvernian Formation during dry climatic periods. The most recent deposits are alluvial soils. Along the Levubu and Limpopo Rivers wide alluvial flood plains occur in which a few pans are located which are periodically filled by floods.

A reconnaissance soil map (Fig. 3) of the northern Kruger National Park was compiled by Harmse, Van Wyk and Gertenbach in 1973. From this map ten main regions can be distinguished within the study area, namely regions with:

- (i) deep sandy soils mainly in the Wambiya area but also in part of the Punda Milia area;
- (ii) sandy loam and clay soils mainly southeast of Punda Milia as well as in the Wambiya area;
- (iii) red clay soils in the Punda Milia area and near Kloppefontein;
- (iv) dark clay soils on the central plains up to the Levubu River in the north;
- (v) medium to heavy soils with a pedocutanic B-horizon north of Punda Milia and west of Pafuri;
- (vi) soils occurring in low-lying areas and along most of the streams in the Punda Milia area and on the flood plains along the Limpopo River;
- (vii) dark clay soils in the low-lying areas occurring mainly on the alluvial flood plains in the Pafuri area;
- (viii) flood plains and dikes in the Pafuri area;
- (ix) shallow soils on granite and sandstone in the Punda Milia and Pafuri areas; and
- (x) shallow calcareous soils and rock, covering large parts of the Punda Milia and Pafuri areas.

A striking correlation exists between the geology and soils of the study area as can be seen by comparing Figures 2 & 3.

Climate

According to Walter (1963) a strong correlation exists between climate and vegetation and Schulze and McGee (1977) stress the fact that the interactions between climatic factors such as light, temperature and rainfall can render the environment suitable for the development of a certain plant community. The temperature amplitudes for Pafuri and Punda Milia are 46.7 °C and 38.3 °C respectively and both extremely high temperatures (November) and relatively low temperatures (July) are experienced. In general the entire area can be regarded as being frost-free. Cyclones which move in sporadically from the



FIG. 3.

Soil map of the Punda Milia—Pafuri—Wambya area in the Kruger National Park
(Drawn after Harmse, Van Wyk and Gertenbach, 1973.)

Mozambique canal influence the rainfall pattern and cause heavy downpours and floods.

According to the classification of the South African Weather Bureau (Schulze, 1965), the study area is part of the climatic region denoted as the Transvaal Lowveld (L). According to the Köppen index it has a BShw climate (Schulze, 1947), where BS = arid steppe climate; h = hot and dry with a mean annual temperature exceeding 18 °C; and w = dry winter. According to the classification of Thornthwaite the study area has a semi-arid, hot (steppe) climate described by the symbols DB'd (Schulze, 1947).

For the discussion of the climate, data from the Weather Bureaus of South Africa and Mozambique are used in Tables 1, 2 & 3 and Figure 4 (Weather Bureau, 1954, 1965; Reparticao tecnica de estatistica, 1961).

LEGEND

Scale 1:480 000



DEEP SANDY SOILS



SANDY LOAM AND CLAY LOAM SOILS



RED CLAY SOILS



DARK CLAY SOILS



MEDIUM TO HEAVY SOILS WITH A PEDOCUTANIC B-HORIZON



SOILS WITH STRUCTURE OF THE LOW LYING AREAS AND DRAINAGE LINES



DARK CLAY SOILS OF THE LOW LYING AREAS



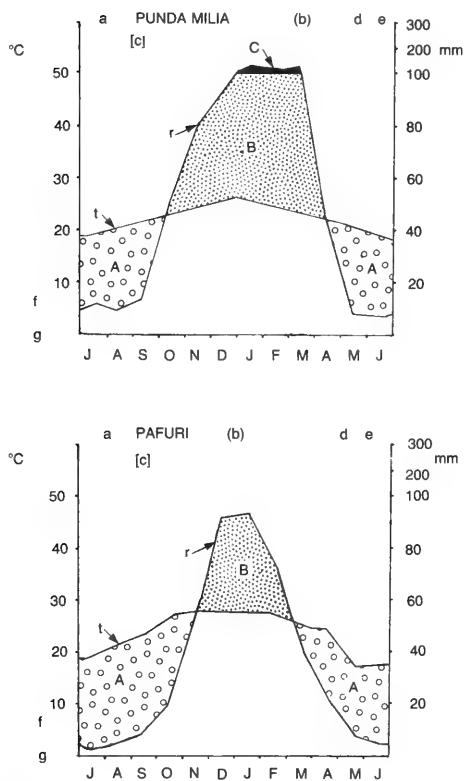
FLOOD PLAINS AND DIKES



SHALLOW SOILS ON GRANITE AND SANDSTONE



SHALLOW CALCAREOUS SOILS AND ROCK



Symbols and explanations

a Weather station

(b) Height above sea level (m)

[c] Years of observation

(First figure for temperature and second figure for rainfall)

d Mean annual temperature (°C)

e Mean annual rainfall (mm)

f Mean daily minimum of the coldest month (°C)

g Absolute minimum (°C)

A Dry period

B Humid period

C Per-humid period

t Mean monthly temperature

r Mean monthly rainfall

	Punda Milia	Pafuri
(b)	462	290
[c]	10—21	10—23
d	22,9	24,2
e	590	415,2
f	11,4	8,1
g	5,0	0,8

FIG. 4.

Climatic diagrams for Punda Milia and Pafuri (Walter and Lieth, 1960; Reparticao tecnica de estatistica, 1961).

Absolute temperatures are probably among the most important factors influencing the distribution of plant species (Van der Schijff, 1957; Schulze and McGee, 1977). Temperatures recorded for Punda Milia range from the absolute maximum of 43,3 °C in December to an absolute minimum of 5 °C in July, with a mean annual temperature of 22,9 °C. For Pafuri the values range from 47,5 °C (November) to 0,8 °C (July) with a mean annual temperature of 24,2 °C (Table 1).

TABLE 1.

Temperature data for Punda Milia (PM) and Pafuri (P) (Mozambique Station) according to the Weather Bureau (1954) and Reparticao tecnica de estatistica (1961)

Month	Weather Station	Temperature in °C for a 10 year period			
		Mean daily maximum	Mean daily minimum	Absolute daily maximum	Absolute daily minimum
January	PM	32,0	19,9	41,1	15,0
	P	33,9	21,4	42,9	13,5
February	PM	30,9	19,9	38,9	15,0
	P	33,8	21,7	44,0	15,5
March	PM	30,0	18,8	38,9	13,3
	P	33,5	20,1	42,2	7,0
April	PM	29,8	16,9	38,3	8,3
	P	32,7	17,3	40,6	10,5
May	PM	27,1	13,6	36,1	7,8
	P	30,7	12,3	40,9	3,8
June	PM	25,2	11,5	32,2	5,6
	P	27,7	8,9	36,3	1,2
July	PM	25,3	11,4	32,2	5,0
	P	28,1	8,1	36,4	0,8
August	PM	27,0	12,9	37,2	6,1
	P	30,1	10,5	39,5	1,0
September	PM	29,3	15,1	38,9	7,8
	P	31,8	14,9	43,5	3,9
October	PM	31,5	17,6	41,1	10,6
	P	34,4	18,9	46,7	8,7
November	PM	31,4	18,9	40,6	11,1
	P	34,1	20,4	47,5	11,6
December	PM	32,9	20,0	43,3	14,4
	P	34,5	21,2	43,5	14,4
Year	PM	29,4	16,4	43,3	5,0
	P	32,1	16,3	47,5	0,8

Punda Milia is situated at 462 m above sea level and has an average annual rainfall of 549,1 mm, whereas Pafuri (Mozambique) lies approximately 290 m above sea level and has an average annual rainfall of 415.2 mm (Table 2). The low-lying and relatively dry Limpopo Valley, in which the Pafuri area is situated, is a zone which is classified as a dry climatic type by Schulze and McGee (1977).

TABLE 2.

The mean monthly and annual rainfall, maximum and minimum monthly rainfall and the mean number of rainy days per month and year for Punda Milia (PM) and Pafuri (P) (Mozambique Station) (Weather Bureau, 1954, 1965; Pienaar, 1973)

Month	Weather Station	Rainfall (mm)				Mean number of rainy days per month
		Mean monthly rainfall	Monthly maximum rainfall	Monthly minimum rainfall	Maximum rainfall in 24 hours	
Period (years)		PM = 41 P = 48	PM = 21 P = 23	PM = 21 P = 23	PM = 17 P = 10	PM = 21 P = 46
January	PM	116.3	436.6	13.6	216.0	7.7
	P	91.0	442.3	2.4	82.9	6.1
February	PM	90.9	286.9	3.0	86.0	7.7
	P	71.2	142.2	—	96.6	5.9
March	PM	84.3	366.1	4.2	89.0	7.0
	P	43.2	120.4	—	43.7	4.8
April	PM	34.0	128.0	0.8	74.0	3.8
	P	21.1	100.3	—	52.0	2.1
May	PM	9.0	58.4	—	12.0	2.1
	P	7.1	54.8	—	10.6	1.2
June	PM	8.0	65.0	—	58.0	1.5
	P	5.3	33.1	—	26.5	1.1
July	PM	6.1	46.0	—	25.0	1.6
	P	1.3	14.0	—	5.8	0.9
August	PM	5.6	61.0	—	57.0	0.8
	P	3.7	6.5	—	0.3	0.9
September	PM	12.7	111.3	—	26.0	1.7
	P	8.5	92.5	—	55.0	1.1
October	PM	23.2	81.0	—	41.0	4.4
	P	17.7	55.3	1.0	26.5	2.4
November	PM	61.5	199.0	3.0	107.0	6.4
	P	56.0	103.0	2.5	57.9	4.9
December	PM	97.5	245.5	3.0	154.0	7.2
	P	89.1	232.9	8.5	56.0	6.0
Year	PM	549.1		—		51.9
	P	415.2		—		37.4

Rainfall and temperature data for Punda Milia and Pafuri are illustrated in the climatic diagrams in Figure 4 (Walter and Lieth, 1960; Reparticao tecnica de estatistica, 1961). The perhumid period, when the monthly rainfall exceeds 100 mm, occurs from the end of December to the middle of March at Punda Milia, but such a period is not experienced at Pafuri. The Punda Milia area has a more humid climate and this is ascribed to the higher humidity and light orographic rainfall which occur more commonly against the escarpment and the south and southeastern side of the Soutpansberg. The mean annual rainfall at Sibasa, approximately 60 km southwest of Punda Milia is 1 163 mm whereas Messina, north of the Soutpansberg has a mean annual rainfall of only 348 mm (Table 3).

TABLE 3.

The mean annual rainfall and mean number of rainy days per year at a number of weather stations in the vicinity of the Punda Milia—Pafuri—Wambya area (Weather Bureau, 1954; Farrell, 1968)

Weather Station	Mean annual rainfall (mm)	Mean number of rainy days per year	Height above sea level (m)	Observation period (years)
Messina	348,0	44,0	549	41
Shingwidzi	410,0	42,6	215	11
Pafuri (Mozambique) ..	415,2	37,4	290	48
Sabi Valley	446,3	—	460	—
Nuanetsi	459,5	—	482	—
Phalaborwa	475,5	47,3	406	43
Punda Milia	549,1	51,9	462	41
Giyani	572,1	44,0	610	9
Triangle	622,0	—	425	—
Louis Trichardt	732,0	75,0	961	41
Levubu	954,1	53,0	610	17
Chipinga	1 118,1	—	1 142	—
Sibasa	1 163,0	66,0	739	49

Thunderstorms frequently occur in the study area and in a 24 hour period as much as 216 mm and 96.6 mm rain have been recorded for Punda Milia and Pafuri respectively. More than 80 % of the total annual rainfall occurs from October to March.

At Punda Milia and Pafuri the cloud cover at 08h00 is highest during February and March and during November and December respectively. According to Van der Schijff (1957) Punda Milia experiences an average of 124,4 days per year with 90 % cloud cover.

Hail seldom occurs and the study area is generally regarded as being frost-free although frost may sporadically occur in low-lying areas. During late summer drizzle is often experienced and dew is regularly formed on clear windless nights.

Biotic factors

The influences of man in the study area include artificial water provision, population control of larger mammals, disease control, tourism, introduction of exotic plants, erection of game proof fences, making of fire breaks, building of tourist roads and aerodromes and the implementation of veld fire policies (Van Wyk, 1975). The grazing and browsing of large mammals, such as buffalo and elephant, sometimes have a visible effect on the vegetation.

METHODS

Considering the size of the study area (1 586 km²) and the heterogeneity of the vegetation it was decided to classify the vegetation on a partly subjective basis using the Braun-Blanquet method (Werger, 1974). By using this method the internal variations and interrelationships between groups of relevés can be presented in a simple way (Coetzee, 1972). The size of the quadrat which was used for the survey of the herbaceous component was 10 m × 20 m (Coetzee and Gertenbach, 1977). The herbaceous component includes all grasses and forbs irrespective of height and semi-woody dwarf shrubs of less than 1 m height.

For the structural analysis of the woody vegetation the Variable Quadrant Plot method of Coetzee and Gertenbach (1977) was employed. This method was used to determine the woody species composition, their trunk diameters, growth forms and height classes and to calculate their maximum canopy spread in different strata, total apparent canopy cover* and number of individuals per hectare. The cover-abundance values of the woody component could also be determined by this method. The size of a quadrat was determined by the density of the vegetation at each sampling plot. The three growth forms of the woody component that were recognised are as follows: tree growth form = individual with a single stem; sparse shrub growth form = individual with two to four stems; shrub growth form = individual with more than four stems.

The following strata were investigated separately: ≤ 0,75 m; > 0,75 – 1,5 m; > 1,5 – 2,5 m; > 2,5 – 3,5 m; > 3,5 – 5,5 m and > 5,5 m. These strata were then termed the 0,5 m; 1 m; 2 m; 3 m; 4–5 m and > 6 m strata respectively.

Homogeneous physiographic-physiognomic areas were mapped on 1: 30 000 aerial photographs. A total of 196 relevés were sampled representing an average density of one relevé for approximately 8 km². The Sandveld and *Colophospermum mopane* communities were analysed floristically as well as structurally, whereas the Hygrophilous communities were only analysed floristically by means of the Braun-Blanquet method. The descriptive phrase included in the name of each community is based on the physiognomic vegetation classification of Tinley (1969).

*Overestimate due to overlapping canopies possible.

RESULTS AND DISCUSSION

During this study (Van Rooyen, 1978) the vegetation of the Punda Milia-Pafuri-Wambya area (Fig. 5 and Table 4) was classified into the following communities.

1. Hygrophilous communities,
2. Sandveld communities,
3. *Colophospermum mopane* communities

In this paper only the Hygrophilous communities are discussed. In part 2 and part 3 of this series the Sandveld and the *Colophospermum mopane* communities respectively will be dealt with.

In Figures 2, 3 and 5 the strong correlation between the geology, soils and vegetation in the study area is shown.

THE HYGROPHILOUS COMMUNITIES

The Hygrophilous communities are found mainly on alluvial soils along rivers and streams. These sandy clay loam to clay soils have a neutral to alkaline pH, with a normal to high soluble salt concentration especially in the vicinity of pans or depressions. Carbonates are often present in these soils.

Two vegetation units were recognised:

1. The *Lonchocarpus capassa*—*Panicum meyerianum* tree savanna
2. The Pan communities

The units differ in terms of structure as well as floristic composition. In the pans themselves the absence of trees and shrubs in the pans is conspicuous while the presence of species such as *Cyperus* spp., *Nymphaea capensis*, *N. caerulea*, *Ottelia exserta* and *Paspalidium obtusifolium* characterise the Pan communities.

The *Lonchocarpus capassa*—*Panicum meyerianum* tree savanna (1) was divided into four communities:

- 1.1 The *Acacia borleae*—*Ischaemum afrum* shrub thicket
- 1.2 The *Combretum imberbe*—*Fuirena pubescens* open tree savanna
- 1.3 The *Acacia albida*—*Ficus sycomorus* riverine forest
- 1.4 The *Acacia xanthophloea*—*Panicum meyerianum* open tree savanna

Community 1.1 is characterised by species group S (Table 4) and the presence of *Setaria sphacelata*, *Ischaemum afrum* and *I. brachyatherum* in this community as well as in the other Hygrophilous communities suggests that these communities are related. Community 1.2, 1.3 and 1.4 are characterised by species group T, U, and V respectively. Species group V is well represented in all the Hygrophilous communities and confirms the relationship between these communities (Table 4). The absence of several species belonging to species groups S, T and U is important in the characterisation of community 1.4.

The salient habitat features of community 1.1 is a heavy clay soil with a well-developed blocky structure while community 1.4 is characterised by a soil with a high pH and high soluble salt concentration.



FIG. 5.
Vegetation map of the Punda Milia—Pafuri—Wambya area in the Kruger National Park.

1.1 The *Acacia borleae*—*Ischaemum afrum* shrub thicket

This community is found at approximately 400 m above sea level on the plains west of Mandadzizi (Figs 5 & 6). Although this community is not found along rivers or streams, the poorly drained and sometimes waterlogged, dark heavy clay soil in the area where it occurs, favours the development of a vegetation type with affinities to other Hygrophilous communities.

The fine textured clay soil has a brown-grey to brown-black colour and is usually deeper than 1 m. The topsoil has a well-developed blocky structure and is moderately to strongly alkaline, with a pH between 8,3 and 8,7. The soil has a moderate to high soluble salt concentration and carbonates are present.

LEGEND

Scale 1:460 000



BURKEA AFRICANA-PSEUDOLACHNOSTYLIS MAPROUNEIFOLIA TREE SAVANNA

BAPHIA MASSAIENSIS-GUIBOURTIA CONJUGATA THICKET



BAPHIA MASSAIENSIS-GUIBOURTIA CONJUGATA THICKET



BAPHIA MASSAIENSIS-XYLIA TORREANA TREE SAVANNA



XERODERRIS STUHLMANNII-COMBRETUM APICULATUM TREE SAVANNA



TERMINALIA SERICEA-POGONARTHRIA SQUARROSA TREE SAVANNA

KIRKIA ACUMINATA-AFZELIA QUANZENSIS-COMBRETUM APICULATUM TREE SAVANNA



KIRKIA ACUMINATA-AFZELIA QUANZENSIS TREE SAVANNA



COMBRETUM APICULATUM-KIRKIA ACUMINATA TREE SAVANNA



ANDROSTACHYS JOHNSONII-CROTON PSEUDOPULCHELLUS DRY FOREST



ROCKY OUTCROP COMMUNITY



MIXED ROCKY OUTCROP COMMUNITY AND ANDROSTACHYS JOHNSONII-CROTON PSEUDOPULCHELLUS DRY FOREST

COLOPHOSPERMUM MOPANE-ACACIA TORTILIS-UROCHLOA MOSAMBICENSIS TREE SAVANNA



ACACIA TORTILIS TREE SAVANNA



ACACIA SENEGAL SHRUB SAVANNA



SALVADORA ANGUSTIFOLIA SHRUB SAVANNA

LEGEND

Scale 1:460 000



COLOPHOSPERMUM MOPANE-EUCLEA DIVINORUM-ENTEROPOGON
MACROSTACHYUS TALL TREE SAVANNA



COLOPHOSPERMUM MOPANE-COMMIPHORA GLANDULOSA-SEDDERA
CAPENSIS OPEN TREE SAVANNA



COLOPHOSPERMUM MOPANE-ENNEAPOGON SCOPARIUS SHRUB SAVANNA



COLOPHOSPERMUM MOPANE-THEMEDA TRIANDRA SHRUB SAVANNA



COLOPHOSPERMUM MOPANE-COMBRETUM APICULATUM-DIGITARIA
ERIANTHA OPEN TREE SAVANNA



DIABASE COMMUNITY



ACACIA BORLEAE-ISCHAEMUM AFRUM SHRUB THICKET



COMBRETUM IMBERBE-FUIRENA PUBESCENS OPEN TREE SAVANNA



ACACIA ALBIDA-FICUS SYCOMORUS RIVERINE FOREST

ACACIA XANTHOPHLOEA-PANICUM MEYERIANUM OPEN TREE SAVANNA



ACACIA XANTHOPHLOEA OPEN TREE SAVANNA



SPOROBOLUS CONSIMILIS GRASSLAND



PAN COMMUNITIES



INTERNATIONAL BORDERS



ROADS



RIVERS

TABLE 4.

A constancy table of the plant communities of the Punda Milia—Pafuri—Wambiya area in the Kruger National Park*

PLANT SPECIES	COMMUNITIES																	
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4	
A <i>Burkea africana</i>	5																	
<i>Fimbristylis hispidula</i>	3			1	1	1						1						
<i>Andropogon gayanus</i>	3					1						1						
<i>Holarrhena pubescens</i>	3																	
<i>Bauhinia galpinii</i>	3				1													
<i>Ochna pulchra</i>	2		1															
B <i>Baphia massaiensis</i>		5																
<i>Grewia microthyrsa</i>		3																
<i>Combretum celastroides</i>		3				1												
<i>Hugonia orientalis</i>		3	1															
<i>Ptaeroxylon obliquum</i>		2																
<i>Pavetta catophylla</i>		2																
<i>Cleistanthus schlechteri</i>		2																
<i>Mariscus</i> sp.		2																
<i>Heinsia crinita</i>	1	2																
<i>Xylia torreana</i>		1																
C <i>Xeroderris stuhlmannii</i>				3														
<i>Aristida junciformis</i>	1		2															
<i>Aristida stipitata</i>	1		3	1														
<i>Indigofera inhambanensis</i>	1		2															
<i>Limeum dinteri</i>			2	1									2					
<i>Macrotyloma axillare</i>			2			1												
<i>Pavonia burchellii</i>			2									1						
<i>Balanites maughamii</i>		1	2		1								2					
D <i>Terminalia sericea</i>	3	2	5	4														
<i>Combretum collinum</i>	3	2	4	3	1								3					
<i>Tricholaena monachne</i>	2	2	3	1	1							1						
<i>Merremia tridentata</i>	4	3	3	3			1	1	1									
<i>Crotalaria sphaerocarpa</i>	1	1	2	3	1			1			1	1						
<i>Perotis patens</i>	3	3	3	3														
<i>Pteleopsis myrtifolia</i>	3	3	2	1	1													
<i>Eragrostis pallens</i>	2	4	2	2														
<i>Zygoon graveolens</i>	1	2	3	3			1											
<i>Aristida argentea</i>	2	2	1	1														

The constancy value of a plant species in a community is indicated by the following symbols: 1 (1–20 %); 2 (>20–40 %); 3 (>40–60 %); 4 (>60–80 %); 5 (>80–100 %)

*The complete differential table can be found in Van Rooyen (1978).

PLANT SPECIES	COMMUNITIES																	
	SANDVELD						COLOPHOSPERMUM MOPANE					DIABASE	HYGROPHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4	
H <i>Combretum zeyheri</i>	3	2	1	3	3	1												
<i>Borreria scabra</i>	1	2	3	1	1	2												
<i>Pogonarthria squarrosa</i>	4	2	2	3	2	1		1				2						
<i>Strychnos decussata</i>	1	2	1	1	1	1												
<i>Pseudolachnostylis maprounei</i> <i>folia</i>	5	1	1	2	2													
<i>Hexalobus monopetalus</i>	2	3	1	1	2													
<i>Strychnos madagascariensis</i> ..	3	2	4	3	3			1		3		1						
<i>Ipomoea magnusiana</i>	2	2	4	2		2	1	1				1						
<i>Guibourtia conjugata</i>	2	5	2		2													
<i>Rhynchosia resinosa</i>		2	3	1	2				1									
<i>Triumfetta pentandra</i>	1			1	2	1		1										
<i>Diplorhynchus condylocarpon</i> ..	4				1	3	1											
<i>Alchornea laxiflora</i>	1	4			2	1												
<i>Monodora junodii</i>	2	2		1	3	1												
<i>Celosia trigynia</i>	1	2			2	2		1										
<i>Waltheria indica</i>	2	2		2	3	1		1	1			2						
<i>Hymenocardia ulmoides</i>	2	2			3	1												
<i>Cassia absus</i>	1			2	1	1												
<i>Blepharis maderaspatensis</i>	1			1	2	2												
<i>Tephrosia elongata</i>	2	1	2	1	1			1										
<i>Rhynchosia venulosa</i>	1	1	2		1	1												
<i>Artabotrys brachypetalus</i>	1	1	1	1	2						1							
<i>Agathisanthemum bojeri</i>	2	2		1	1			1										
<i>Tephrosia longipes</i>	2		1	1	1							1						
<i>Crabbea velutina</i>	1		2		1	1		1					2					
<i>Hippocratea longipedunculata</i> ..		1	1	1	1													
<i>Ximenia caffra</i>	1			1														
<i>Ozoroa paniculosa</i>	1				1						1							
<i>Ozoroa engleri</i>			1	1														
I <i>Urochloa mosambicensis</i>				1			5	1		1	1	2		4	2			
<i>Chloris virgata</i>				1			4	1	1					2				
<i>Acacia tortilis</i>							3	1										
<i>Salvadora angustifolia</i>							2		1						2		1	
<i>Boerhavia diffusa</i>							2										1	
<i>Azima tetracantha</i>							2											
<i>Alternanthera pungens</i>							1											
<i>Trianthema triquetra</i>							1											
<i>Setaria verticillata</i>							1											
<i>Acacia senegal</i>					1		1											
<i>Cyathula crispula</i>							1											
J <i>Ximenia americana</i>			1	1			1	4										
<i>Enteropogon macrostachyus</i> ..					1	2	1	3	1									

PLANT SPECIES	COMMUNITIES																
	SANDVELD					COLOPHOSPERM MOPANE					DIABASE	HYGROPHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Tetrapogon tenellus</i>							1	2									
<i>Chloris roxburghiana</i>							1	2									
<i>Acacia grandicornuta</i>							2	1									
<i>Amaranthus thunbergii</i>							1	1									
K <i>Commiphora glandulosa</i>					1		2	1	3		1						
<i>Abutilon fruticosum</i>					1	1	2	2	2								
<i>Ecobolium revolutum</i>							2	2	2								
<i>Sporobolus smutsii</i>	1			1	1		2	1	1								
<i>Thilachium africanum</i>				1			2	1	1				2				
<i>Corbichonia decumbens</i>							1	1	2								
<i>Sporobolus fimbriatus</i>							1	1	1								
<i>Aristida rhiniochloa</i>							1	1	1								
L <i>Enneapogon scoparius</i>										5							
<i>Euclea schimperii</i>				1						4							
M <i>Terminalia prunioides</i>							1	3	2	3							
<i>Maerua parvifolia</i>				2	1		3	3	2	1			2				
<i>Seddera capensis</i>							1	2	3	5	1	1					
<i>Elytraria acaulis</i>								2	2			1					
<i>Zanthoxylum capense</i>							1	1	2	2							
N <i>Themeda triandra</i>								1			5		2				
<i>Neorautanenia amboensis</i>								1	1		4						
<i>Setaria woodii</i>							1	1	1		3						
<i>Urochloa brachyura</i>								1			2						
<i>Panicum coloratum</i>											2			3			
O <i>Heteropogon contortus</i>	1				1			1	2	4	4	2	2		2		
<i>Bothriochloa insculpta</i>							1	2	3		4		2		2		
<i>Phyllanthus maderaspatensis</i> . .								1	2	2	1	1					
<i>Fingerhuthia africana</i>								1	2	3	1	2					
<i>Indigofera heterotricha</i>								1	2	1	2	1					
<i>Sorghum versicolor</i>								1	2		3	1					
<i>Heliotropium strigosum</i>				2				2			2	1					
<i>Oropetium capense</i>								1	1	1	1	1					
P <i>Colophospermum mopane</i>				2	1		3	5	5	5	5	5		5	4		
<i>Euclea divinorum</i>	1			1			1	3	1	2		1		5	3		
<i>Aristida congesta</i> subsp. <i>barbicollis</i>																	
<i>Neuracanthus africanus</i>				1			1	2	3	2	3	2					
<i>Barleria lancifolia</i>				1			1	2	4	1	1	2					
<i>Eragrostis rigidior</i>		1		1	1		1	2	2	2	2	1					

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2		3	4	1.1	1.2	1.3
<i>Eragrostis superba</i>							1	1	1	2	4	1					1
<i>Combretum hereroense</i>					1		1	1	1	1	1	3		2			1
<i>Dicoma tomentosa</i>							1	1	1		1	1					
<i>Dalechampia galpinii</i>								1	2								
<i>Aptosimum lineare</i>								1	2								
<i>Sterculia rogersii</i>					1				1	2		1					
Q <i>Combretum apiculatum</i>	2	2	5	4	5	1	1	1	5	4	2	5					
<i>Aristida congesta</i> subsp. <i>con-</i> <i>gesta</i>	1	2	3	3	2	2	3	4	5	5	3	3		2			
<i>Indigofera vicioides</i>	1	3	1	1	1	1	1	2	3	4	2	2					
<i>Cissus lonicerifolius</i>	1	2	2	2	1	1	1	1	3	1	2	2					
<i>Hermannia glanduligera</i>	3	2	1	3	2	1	1	1	1	2	1	3					
<i>Rhynchosia totta</i>	3	1	2		1	1	1	1	3	3	2	2	3				
<i>Phyllanthus burchellii</i>	1	5	3	1	1	3		1	3		1	2	2				
<i>Hibiscus engleri</i>	2	2	2	2	2	2	2	1		1	1	1		2			
<i>Brachiaria nigropedata</i>	2	3	1	3	1	1		1	1		2	2					
<i>Vigna unguiculata</i>	3	2	4	4	1	1	1	1			2	2					
<i>Commelina africana</i>	2		2	1	1	1	2	1			1	1					
<i>Acalypha indica</i>	1		1	2	1	1	2	1	2	2	1	1	2				
<i>Boscia albitrunca</i>	1	1	2	3	2	1	1	1	1			2					
<i>Commelina erecta</i>	2	3	1	2	2	1	2	1				2					
<i>Monechma monechmoides</i>		1	3	2	1	2	1	1	3		1	1					
<i>Enneapogon cenchroides</i>	1		1	3	2	1	3	4	5	2	2	2					
<i>Phyllanthus pentandrus</i>	1		1	1	1	1	1	2	1	4	1	3					
<i>Tephrosia polystachya</i>	1	2	5	3	1	1		1	3	3	2	3					
<i>Cassia abbreviata</i>	1	1	1		1	1			1		1	1					
<i>Schmidtia pappophoroides</i>	2	2	4	4	1			2	2		3	4					
<i>Hibiscus sidifolius</i>		1	1	1	1	2	1	1	2			2					
<i>Kyphocarpa angustifolia</i>	1	1	1	1	3			1	2	1		2					
<i>Grewia bicolor</i>	1	2	2	2	1	3	4	4	4	4	2	3	2				
<i>Dalbergia melanoxylon</i>	2		4	3	1		1	1	1	4	3	2					
<i>Pseudobrachiaria deflexa</i>		2			1	3	2	1	3		1	1					
<i>Pupalia lappacea</i>	1			2	2	3	3	1	2				2				
<i>Evolvulus alsinoides</i>	1	1	1	2	2	1		3	2		1	1					
<i>Tragus berteronianus</i>			1	1	1		3	1	1	1	1	1					
<i>Cassia mimosoides</i>	1			2		1		1			2	1					
<i>Euphorbia polycnemoides</i>	1			1	3	1		1	3	2	1	2					
<i>Crotalaria virgulata</i>		1	1	1		1		2	1			2					
<i>Euphorbia tetensis</i>	2		3	2				1	3	1	1	2					
<i>Maytenus heterophylla</i>			1		1		1	1	1	4	1	1					
<i>Cucumis anguria</i>				2		1	1	1	1		1	1	2				
<i>Corchorus asplenifolius</i>	1			3		1	1		2	2	1	1	2	3			
<i>Lantana rugosa</i>	2		1		1	1			1			2					
<i>Tricalysia allenii</i>	1	1		1	2				1			1					

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Ipomoea obscura</i>				1		1	2	1	1		1	1					
<i>Grewia monticola</i>			3	1	1	1		1			1	1					
<i>Mundulea sericea</i>	1		1	1	1				1		1	1					
<i>Cymbopogon excavatus</i>				1					1	1	2	1	3	2			
<i>Markhamia acuminata</i>				2	1				1		1	1					
<i>Gardenia resiniflua</i>				1	1	1	1	1	1								
<i>Justicia protracta</i>	1							1	1								
<i>Barleria affinis</i>					1				1								
<i>Stylochiton natalensis</i>	1				1	1		1									
<i>Eragrostis curvula</i>				1				1				1					
<i>Ipomoea pes-tigrides</i>	1	2		1			1	1									
<i>Zornia diphylla</i>	1	2		1	1				1			1					
<i>Clerodendron ternatum</i>	1		1	1				1	1	1	1	1					
<i>Justicia flava</i>					1		1	1				1					
<i>Manilkara mochisia</i>	1			1	1				1								
<i>Rhynchosia minima</i>	1							1			1	1					
<i>Eragrostis heteromera</i>				1			1		1								
<i>Grewia hexamita</i>		1	1	1	1	1			1		1		2				
<i>Gisekia africana</i>				1			2				1						
<i>Commiphora edulis</i>					1	1			1								
<i>Anisotes sessiliflorus</i>		1			1		1	1	1								
<i>Cardiospermum halicacabum</i>					1				1								
<i>Aspilia mossambicensis</i>	1								1			1					
<i>Dactyloctenium aegyptium</i>				1			1										
<i>Polygala wilmsii</i>	2		1		1				1		1						
<i>Calostephane divaricatum</i>				1	1			1	1								
<i>Hermbstaedtia odorata</i>	1							1		1		1					
<i>Kyllinga alba</i>	1					1		1			1	1					
<i>Kohautia virgata</i>	2						1	1		1		1					
<i>Gardenia spatulifolia</i>			1	1		1											
<i>Cissus quadrangularis</i>					1	1	1	1									
<i>Stipagrostis uniplumis</i>	1			1				1	1		1						
<i>Eragrostis lehmanniana</i>				1				1	1								
<i>Leptactinia benguelensis</i>		1	1		1	1		1									
<i>Ipomoea crassipes</i>											1						
<i>Orthosiphon suffrutescens</i>								1	1								
<i>Grewia villosa</i>					1	1	1		1		1						
<i>Lippia javanica</i>								1	1		1		2				
<i>Merremia palmata</i>											1	1					
<i>Endostemon tenuiflorus</i>									1	1							
R <i>Setaria holstii</i>													4	3	2		
<i>Piliostigma thonningii</i>													3				
<i>Hyparrhenia rufa</i>													3				
<i>Helichrysium miconiifolium</i>													3				

PLANT SPECIES	COMMUNITIES																	
	SANDVELD						COLOPHOSPER- MUM MOPANE						DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4	
<i>Ipomoea papilio</i>						1							3					
<i>Acacia gerrardii</i>											1		2					
S <i>Acacia borleae</i>														5				
<i>Tetrapogon mossambicensis</i> ..								1						5				
<i>Cephalocroton mollis</i>											1			5				
<i>Ruellia patula</i>				1			1	1	1		1	1		5				
<i>Brachiaria erucaeformis</i>														5				
														3				
T <i>Sesbania sesban</i>															4			
<i>Fuirena pubescens</i>															3			
U <i>Acacia albida</i>																5		
<i>Ficus sycomorus</i>																4		
<i>Acacia robusta</i>																4		
<i>Trichilia emetica</i>																4		
<i>Diospyros mespiliformis</i>																4		
<i>Hypoestes verticillaris</i>																3		
<i>Abutilon angulatum</i>																3		
<i>Tabernaemontana elegans</i>	1				1											3		
V <i>Setaria sphacelata</i>									1			1	2	3	3		3	
<i>Ischaemum afrum</i>														5	4		2	
<i>Ischaemum brachyatherum</i> ...														3	2		1	
<i>Panicum meyerianum</i>															4	3	4	
<i>Echinochloa pyramidalis</i>															3	2	2	
<i>Acacia xanthophloea</i>																3	1	
<i>Sporobolus consimilis</i>																2	2	
<i>Xanthocercis zambesiaca</i>																3	1	
<i>Kigelia africana</i>																2	1	
<i>Cyperus fenzelianus</i>																	2	
<i>Croton megalobotrys</i>																	1	
<i>Chloris gayana</i>	1																1	
W <i>Panicum maximum</i>	4	5	5	5	4	3	5	4	4	1	3	4	2	4	5		3	
<i>Digitaria eriantha</i>	5	4	5	5	5	2	1	3	4	4	5	5	2	3	3	4		
<i>Hibiscus micranthus</i>	1	1	2	2	3	3	3	4	5	3	1	4		2				
<i>Lonchocarpus capassa</i>	1	1		3	1	1	1	1			2		3		4	4	2	
<i>Spirostachys africana</i>	1	3	1	1	1		1	2						4	4		1	
<i>Combretum imberbe</i>				1			1	1	1	1	3	1	2		3	3	2	
<i>Solanum panduraeforme</i>	2			2	2	2	1	1	2	2	1	2	3		2		1	
<i>Dichrostachys cinerea</i>	2	3	1	3	2	1	1	1	2	2	2	3	4	4	2		1	
<i>Combretum mossambicensis</i> ..	1	2	2	3	1	1	1	1	2	1	2	2	2				1	
<i>Acacia nigrescens</i>	1			2	2		2	3	3	4	2	4	3		4			
<i>Securinega virosa</i>		2	1	1	1		1	1	1		1	1		5			1	

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE		HYGRO- PHILOUS			
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Vernonia fastigiata</i>	4			1	2	2	1	1	2	1	3	1	5				
<i>Cenchrus ciliaris</i>			1					1	2		2	1					1
<i>Achyranthes aspera</i>	1			1	1	3	1	1	1							5	1
<i>Indigofera rhytidocarpa</i>	1	1		2			3	1	1	2	1	1					
<i>Lannea stuhlmannii</i>		2	1	1			1	1	1		1	1			2		
<i>Leucas glabrata</i>	1		1	2	1	1	1	1	2								1
<i>Melhania forbesii</i>	1	1	3	2	1			2	1	1	1	2					1
<i>Monechma divaricatum</i>				1	2		1	1									
<i>Sclerocarya caffra</i>	1	1	2	1	1					1	1	1					
<i>Rhynchelytrum villosum</i>			1	2	1	2		1	2	3	1	1	2		2		
<i>Commiphora mollis</i>				2				1	2	2		1					
<i>Becium obovatum</i>				1		1	1	1	3			1					
<i>Asparagus setaceus</i>	1			1	1	2		2	1	1		1	3				
<i>Corchorus kirkii</i>			2	2	1	1		1	1		1	1			3		1
<i>Tragia rupestris</i>	1		1	1	1			1	1		1	2			2		1
<i>Grewia flavescens</i>		2		1	1	1										2	
<i>Maytenus senegalensis</i>				1									2				1
<i>Leonotis nepetifolia</i>	2			1	1	1						2					1
<i>Pterocarpus rotundifolius</i>											1	2					
<i>Ceratotheca triloba</i>				1			1		1		1				2		
<i>Barleria transvaalensis</i>							1	1	1								
<i>Peltophorum africanum</i>	2				1				1				2				
<i>Hemizygia bracteosa</i>	1	1	2	1	1					1		1			2		
<i>Albizia harveyi</i>												1			2		
<i>Abutilon guineense</i>				1	1		1	1	1				2				1
<i>Ziziphus mucronata</i>				1	1		1	1		1		1					1
<i>Melhania rehmannii</i>				1	1	1		1			1						1
<i>Cyperus</i> sp.				1			1	1		1					2		
<i>Ormocarpum trichocarpum</i> ...								1				1	2		2		
<i>Abutilon ramosum</i>							1				1		2				1
<i>Indigofera schimperi</i>	1				1						1	1	3	2			
<i>Cassia petersiana</i>	1	1	1	1							1		2				

Trees in this shrub thicket are scarce and shrubs and sparse shrubs grow up to 3 m high. The most conspicuous species are *Colophospermum mopane* and *Acacia borleae*, although *Euclea divinorum* and *Securinega virosa* occur more widespread. The limited variety of woody plant species is diagnostic. The herbs have a low canopy cover and the most common species are *Ischaemum afrum* and *Tetrapogon mossambicensis*. A few other herbaceous species that are frequently found are *Cephalocroton mollis*, *Brachiaria eruciformis*, *Ruellia patula*, *Corchorus asplenifolius* and *Panicum coloratum*. Widespread and abundant spe-



FIG. 6.

The *Colophospermum mopane*—*Acacia borleae* shrub savanna on the plains south of Klopperfontein.

cies such as *Panicum maximum* and *Digitaria eriantha* do not commonly occur in this community.

1.2 The *Combretum imberbe*—*Fuirena pubescens* open tree savanna

This community is situated at approximately 385 to 445 m above sea level along streams and near fountains in the Punda Milia area (Figs 5 & 7). The dark red-brown to brown-black soils which vary from a sandy clay loam to clay, are fine textured and usually more than 1 m deep. The topsoil has a moderately developed blocky structure and a friable consistency. The pH of the soil ranges from 6.0 to 6.8. The concentration of dissolved salts is moderate and in most cases a low concentration of carbonates is present in the soil. There is no striking difference between the habitat of this community and the other Hygrophilous communities except for a more neutral pH of the soil.

This community is characterised by sparsely distributed trees, a few shrubs and a grass stratum up to 1.5 m in height and the most striking species, such as *Combretum imberbe*, *Lonchocarpus capassa* and *Spirostachys africana* occur throughout the savanna. The most conspicuous shrubs are *Euclea divinorum*, *Dichrostachys cinerea* and *Albizia harveyi*. Common herbs include *Sesbania sesban*, *Fuirena pubescens*, *Ischaemum afrum* and *Panicum maximum*, while spe-



FIG. 7.

The *Combretum imberbe*—*Fuirena pubescens* open tree savanna along the streams near Punda Milia.

cies such as *Cyperus sphaerospermus*, *Ammania senegalensis*, *Lotononis solitudinus*, *Ageratum conyzoides* and *Gomphrena celosioides* have low constancy values.

1.3 The *Acacia albida*—*Ficus sycomorus* riverine forest

The forest occurs between 197 m and 215 m above sea level on alluvial soils on the banks of the Limpopo and Levubu Rivers and a few of their tributaries. It is also present around several of the perennial fountains west of Punda Milia (Figs 5 & 8).

The community occurs on fine textured dark red-brown to brown-black sandy loam, sandy clay or clay soils. The soil is more than 1 m deep and the topsoil is either apedal or has a weak blocky structure with a loose to friable consistency. The pH of the soil ranges from 7,2 to 7,6 and the topsoil contains a moderate concentration of soluble salts and is neutral or leached.

Trees in this community are up to 20 m high and sometimes form an almost closed canopy. In some places a dense shrub thicket up to 3 m develops beneath the trees. Physiognomically the most noteworthy species are *Acacia albida*, *A.*



FIG. 8.

The *Acacia albida*—*Ficus sycomorus* riverine forest along the Levubu River.

robusta, *Ficus sycomorus*, *Trichilia emetica* and *Xanthocercis zambesiaca*. Conspicuous shrubs and sparse shrubs include *Grewia flavescens*, *G. caffra*, *G. inaequilatera*, *Pluchea dioscorides*, *Ficus capreifolia*, *Acacia schweinfurthii* and *Combretum paniculosa* subsp. *microphyllum*. The herbaceous component consists mainly of species favouring disturbed areas. According to Van der Schijff (1957) this can possibly be attributed to sporadic floods with the accompanying silt deposition. Common herbaceous species include *Panicum maximum* and *Digitaria eriantha* with high constancy values and *Abutilon angolense*, *Achyranthes aspera*, *Epaltes gariepina* and *Hypoestes verticillaris*.

Other widespread herbs are *Wissadula rostrata*, *Ageratum conyzoides*, *Cymbosetaria sagittifolia* and *Senecio inaequidens*.

The riverine forest is better developed and denser along the Levubu than along the Limpopo River. Where the Levubu cuts through the Waterberg and Cave Sandstone a number of species are found that are scarce along the Limpopo River, e.g. *Rauvolfia caffra*, *Ekebergia capensis*, *Breonadia microcephala*, *Strychnos potatorum*, *Syzygium guineense* and *Deinbollia oblongifolia*.

From Lanner Gorge to the confluence of the Levubu River and Limpopo River, characteristic vegetation zones have developed parallel to the Levubu

River. These zones are not always continuous and do not always have the same pattern, but in general four zones can be distinguished:

- (a) In the water or at the water's edge species such as *Ficus capreifolia*, *Phragmites australis* and *Cyperus sexangularis* grow;
- (b) high trees on the river bank, including species such as *Ficus sycomorus*, *Acacia albida*, *A. robusta*, *Garcinia livingstonei* and *Trichilia emetica*;
- (c) semi-hygrophilous species further away from the river bank such as *Acacia xanthophloea*, *Combretum imberbe*, *Croton megalobotrys*, *Kigelia africana*, *Hyphaene natalensis*, *Lonchocarpus capassa*, *Xanthocercis zambsesiaca*, *Albizia versicolor* and *Maclura africana*; and
- (d) the *Acacia tortilis* zone which is the farthest from the water where species such as *A. tortilis*, *A. nilotica*, *Azima tetracantha*, *Capparis sepiaria* and *Xanthocercis zambsesiaca* occur.

1.4 The *Acacia xanthophloea*-*Panicum meyerianum* open tree savanna

This community occurs between 200 and 415 m above sea level on the alluvial plains along the Levubu and Limpopo rivers (Figs 5 & 9).

The fine textured alluvial sandy clay loam, sandy clay or clay soils are brown-black to black and range from 600 to more than 1 000 mm in depth. The topsoil has a weak to moderate blocky structure and a friable to firm consistency. An outstanding feature of the habitat is the generally alkaline soils with a pH of up



FIG. 9.

Flood plains with sparsely distributed trees like *Acacia xanthophloea* and *Sporobolus consimilis* as the most conspicuous grass species.

to 9.9 and with a high concentration of soluble salts. Carbonates are usually found in the soil.

Trees are from 6 to 15 m high and occur widespread throughout the flood plains and on the edge of the flood pans. In some places dense stands of a single species have developed, e.g. the *Acacia xanthophloea* forest near Crook's Corner. Dense stands of *Diospyros mespiliformis* as well as *Combretum imberbe* are also found. Although the shrub layer is not well developed it becomes 2 m high and the most conspicuous species are *Dichrostachys cinerea*, *Securinega virosa* and *Combretum mossambicensis*. Other woody species in this community include *Lonchocarpus capassa*, *Combretum hereroense*, *Croton megalobotrys*, *Maytenus senegalensis*, *Ziziphus mucronata* and *Spirostachys africana*.

Large parts of the flood plains are densely overgrown with grass species becoming up to 2 m high. The most conspicuous species are *Sporobolus consimilis*, *Setaria sphacelata*, *S. holstii*, *Panicum meyerianum*, *P. deustum*, *P. maximum* and *Ischaemum afrum*. Dense stands of only one or two of these species occur regularly.

In Figure 5 this community is subdivided into the *Sporobolus consimilis* grassland and the *Acacia xanthophloea* open tree savanna. According to Rattray and Wild (1955) the presence of *Acacia xanthophloea* in a region is indicative of the existence of a high water table and waterlogged soils.

2. Pan Communities

The pans along the Limpopo and Levubu Rivers are either filled during thunderstorms or are sporadically flooded. These pans are situated in the *Acacia xanthophloea*-*Panicum meyerianum* open tree savanna (1.4) and trees growing on the edge of these pans include species such as *Acacia xanthophloea*, *Combretum imberbe*, *Lonchocarpus capassa* and *Hyphaene natalensis*. In and around the pans in the Pafuri area the following species are characteristic:

<i>Sporobolus consimilis</i>	<i>Cyperus corymbosus</i>
<i>Panicum meyerianum</i>	<i>C. sexangularis</i>
<i>Ischaemum afrum</i>	<i>C. immensus</i>
<i>Setaria sphacelata</i>	<i>C. distans</i>
<i>Cyperus fastigiatus</i>	<i>Nymphaea caerulea</i>

In the Wambya area the pans are filled by rain (Fig. 10) and the most striking species in and around the pans are:

<i>Nymphaea capensis</i>	<i>Bergia salaria</i>
<i>N. caerulea</i>	<i>Epaltes gariepina</i>
<i>Ottelia exserta</i>	<i>Cyperus difformis</i>
<i>Paspalidium obtusifolium</i>	<i>Fuirena ciliaris</i>
<i>Neptunia oleracea</i>	<i>Vahlia capensis</i>



FIG. 10.
Machayi pan in the Wambya area.

The vegetation in the immediate vicinity of the Wambya pans differs markedly from the surrounding Sandveld vegetation and the most conspicuous species are:

<i>Spirostachys africana</i>	<i>Dichrostachys cinerea</i>
<i>Combretum imberbe</i>	<i>Euphorbia ingens</i>
<i>Diospyros mespiliformis</i>	<i>Ehretia amoena</i>
<i>Lonchocarpus capassa</i>	<i>Gardenia spatulifolia</i>
<i>Dalbergia melanoxylon</i>	<i>Crossopteryx febrifuga</i>

These species also occur on termitaria in the Sandveld regions.

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DIE ANATOMIE VAN DIE PINNAS VAN DIE SUID-AFRIKAANSE SPESIES VAN *ENCEPHALARTOS* LEHM.

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UITTREKSEL

Die anatomie van die pinnas van die Suid-Afrikaanse *Encephalartos*-spesies word bespreek en 'n identifikasiesleutel wat op die anatomiese kenmerke van die pinnas gebaseer is word aangebied. 'n Gedeelte van die pinna is voldoende om identifisering met behulp van hierdie sleutel te bewerkstellig. Moontlike ontwikkelingslyne wat op 'n verband tussen blaarkenmerke en geografiese verspreiding berus, word bespreek.

ABSTRACT

THE ANATOMY OF THE PINNAE OF THE SOUTH AFRICAN SPECIES OF *ENCEPHALARTOS* LEHM.

The anatomy of the pinnae of the South African *Encephalartos* species is discussed. An identification key based on anatomical characteristics of the pinnae is presented. South African species of *Encephalartos* can be identified from portions of leaves with the aid of this key. Possible evolutionary lines based on the relation between leaf features and geographical distribution are discussed.

INLEIDING

Encephalartos-spesies word tans in Suid-Afrika as bedreigde plantsoorte beskou en word in al die Provinsies beskerm, maar volgens Artikel 85A van Ordonnansie 17 van 1967 is hulle in die Transvaal as spesiaal-beskermde plante verklaar. Dit is gebruikelik om plante se blare te verwyder wanneer hulle vervoer en oorgeplant word, met die gevolg dat dit haas onmoontlik is om die ontblaaarde plante tot op spesiesvlak te identifiseer. Vir die doeltreffende toepassing van die Ordonnansie is dit noodsaaklik dat plante ten alle tye identifiseerbaar moet wees en daar moes dus gesoek word na alternatiewe kenmerke. Daar is op anatomiese kenmerke van die basale gedeelte van die blaarsteel besluit omdat dié gedeeltes van die blaar normaalweg nie saam met die res van die blaar verwyder word nie. Die anatomie van die pinnas is ook by die ondersoek ingesluit terwille van 'n volledige anatomiese beeld van die blare. Hierdie artikel handel slegs oor laasgenoemde aspek terwyl eersgenoemde in 'n volgende artikel behandel sal word.

MATERIAAL EN METODE

Die materiaal wat ondersoek is, het bestaan uit segmente van die pinnas geneem tussen tien tot dertig mm vanaf die basis.

Die meeste van die materiaal is uit die botaniese tuin van die Navorsingsinstituut vir Plantkunde te Brummeria, Pretoria, verkry van plante wat deur Dyer vir sy beskrywings van die Suid-Afrikaanse *Encephalartos*-soorte gebruik is (Dyer, 1965). Die Afdeling Natuurbewaring van Transvaal het materiaal afkomstig van plante uit die natuurreserve verskaf en materiaal is ook van plante wat in die botaniese tuine van die Universiteit van Pretoria en van die Universiteit van Suid-Afrika aangeplant is, verkry. Materiaal van 'n aantal Kaapse spesies is in die veld in die tipelokaliteite versamel. Herbariummonsters van die plante wat bestudeer is, sowel as anatomiepreparate word in die Schweickerdt Herbarium, Departement Plantkunde, Universiteit van Pretoria, bewaar. 'n Volledige lys van die materiaal wat vir die ondersoek gebruik is, verskyn in die bylaag.

Omdat die materiaal baie hard is, is dit vir 10 tot 30 minute in 'n 10% KOH-oplossing gekook voordat dit in 'n tersiêre-butilalkohol-reeks gedehidreer en in paraplast-was met 'n smeltpunt van 57 °C, volgens die metode van Johansen (1940) geïmpregneer en ingebed is. Materiaal wat nie goeie sneë met bogenoemde metode opgelewer het nie is in die wasblokkies vir een tot twee weke of selfs langer met die snyvlak na onder in 'n houër met Mollifex geplaas om dit sagter te maak.

Dwarssneë van 10 µm tot 15 µm is met 'n roterende mikrotroom gemaak, met safranien en kleurvaste groen gekleur, in kanadabalsem gemonteer en daarna met 'n Leitz Wetzlar ligmikroskoop ondersoek. Die ad- en abaksiale vlakke van die pinnas van 'n aantal *Encephalartos*-soorte is ook met behulp van 'n aftaselektronmikroskoop ondersoek (Fig. 4 en 5).

DIE ANATOMIE VAN DIE PINNAS

Algemeen

Die pinnas van meeste van die ondersoekte spesies is dorsiventraal. Onder dié spesies met dorsiventrale pinnas is daar 'n aantal wat palissadeselle aan albei kante besit maar die palissadeselle aan die abaksiale kant is of in groepies gerangskik byvoorbeeld *E. lehmannii* (Fig. 10 A), of hulle is korter en kleiner as dié aan die adaksiale kant, of 'n kombinasie van laasgenoemde twee, kom voor. *E. eugene-maraisii* (Fig. 3 A) en *E. cupidus* (Fig. 3 B) is die twee uitsonderings met isobilaterale pinnas. Hierdie en ook ander kenmerke word onder die betrokke hoofde bespreek.

Kutikula

Al die spesies besit 'n dik kutikula wat die kontoer van die epidermis volg. Dit kan ook duidelik waargeneem word dat die kutikula van die adaksiale

OORSPRONG EN VERWYSINGS VAN MATERIAAL WAT GEBRUIK IS

BYLAAG

Encephalartos = spesie	NIP	NB	NAT	UP	Unisa	Self versamel in Tipe-lok.	Schw.-Herb. Nr. en Preparaatnommer
<i>E. altensteinii</i>	2952				Alexandria	Trappe's Valley	30913, 30918, 35929, 35930
<i>E. arenarius</i>	10383		Alexandria			Kaba Vallci	30907, 30913, 30975
<i>E. caffer</i>	5556					Brooklands	30911, 30976, 36942
<i>E. cupidus</i>			Penge	UP		Grahamstad	36964
<i>E. cycadifolius</i>				UP	Craddock		30895, 36973-5
<i>E. eugene-maraisii</i>	3336		Mica	Wolkberg			37231-3
<i>E. ferax</i>	6440		Middelburg	Waterberg		Mica	30961, 36979-81, 36985
<i>E. friderici-guilelmi</i>	6981		Kosibaai		Kosibaai	Middelburg	30888, 30978, 35931
<i>E. ghellinckii</i>	6667		Pondoland	UP		Cathcart	30903, 37373, 37374
<i>E. heenanii</i>	15566		Barborton	UP		Pondoland	30905, 36943, 36955
<i>E. horridus</i>	898		Uitenhage	UP	Uitenhage		30882, 30908, 36957-8, 36969
<i>E. humilis</i>			Makubolaan	UP			30920, 35924, 36954
<i>E. inopinus</i>	3326		Penge	Penge			30890, 37236-7
<i>E. laevifolius</i>			Berlin				30912, 37234-5
<i>E. lancatus</i>	3331		Middelburg				30884, 30921, 36965-7
<i>E. latifrons</i>	728		Pongola	UP	Trappe's Valley		30889, 36951, 36959-61
<i>E. lebomboensis</i>	11296		Kommadagga	Jansenville			30981, 36945, 36948
<i>E. lehmannii</i>							30883, 30979, 36986
<i>E. longifolius</i>	11300						30887, 30974, 35921-3, 35920, 35933-4
<i>E. natalensis</i>	11299	3	Barborton		Joubertina		30917, 35935, 35936
<i>E. ngyanus</i>	11297				Vryheid Dist.		35937, 36939, 36946-7
<i>E. paucidentatus</i>			Ida Doyer	Barborton			30909, 36944, 37403
<i>E. princeps</i>	11294			Komga	Barborton		30892, 30902, 35926, 35927-8, 36941, 36962-3
<i>E. transvenosus</i>	277		Modjadja		Komga		30897, 35938, 35925, 36952, 36976-8
<i>E. trispinosus</i>	11291		Pluto's Vale				36952, 36976-8
<i>E. umbeluziensis</i>	3332	3	Barborton	Umbeluzivallei			30906, 30915, 36940, 36953
<i>E. villosus</i>	1517	3		Durban	Bathurst	Pluto's Vale	30896, 30899, 36970-2
<i>E. woodii</i>	5557				Port St Johns		30910, 30980, 31017
					Durban		30919, 35932, 36949
							30893, 30904, 36956, 36982-4
							30977, 35918, 35919

NIP Navorsingsinstituut vir Plantkunde; NAT Afdeling Natuurbewaring;
 UP Universiteit van Pretoria; Unisa Universiteit van Suid-Afrika
 NB Afdeling Natuurbewaring van die Transvaalse Provinsiale Administrasie (Kwekery te Hartbeeshoek)

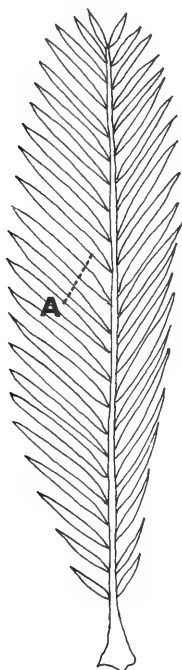


FIG. 1

Skets van 'n *Encephalartos*-blaar. A dui die plek aan waar materiaal geneem is.

epidermis by die meeste soorte effens dikker is as dié van die abaksiale epidermis. Die kutikula volg die kontoer van die epidermis tot in die epistomatale holte en loop dood op die sluitselle.

Epidermis

Die epidermis bestaan uit een laag betreklik klein selle waarvan die buitenste tangensiale wande meer verdik is as die ander wande. By sekere spesies byvoorbeeld *E. horridus* (Fig. 10 B) is die adaksiale epidermisselle kleiner as dié aan die abaksiale kant. Die selle varieer wat vorm betref maar hulle is meestal of sirkelvormig in deursnee of min of meer reghoekig met afgeronde hoeke.

Die meeste van die spesies se pinnae is hipostomaties. Die stomas kom in rye oor die lengte van die pinna in die interkostale gedeelte voor. Gewoonlik is daar twee tot vier rye stomas per interkostale streek, maar ook hier is daar variasie tussen sekere spesies opgemerk. *E. friderici-guilielmi* (Fig. 8 B) het een tot twee

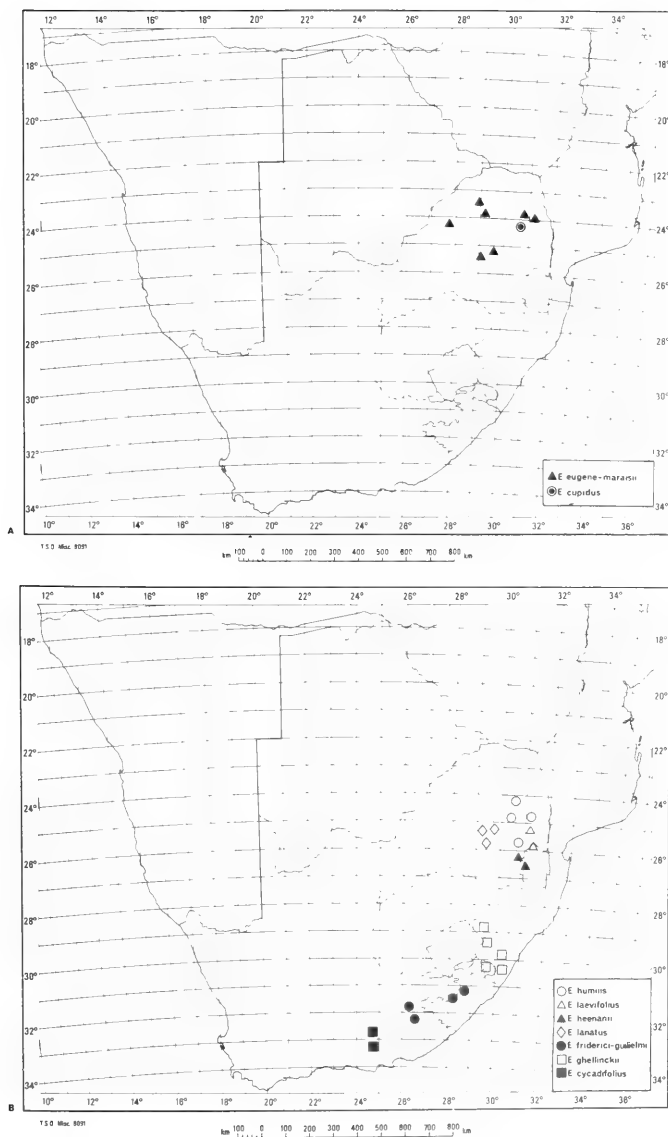
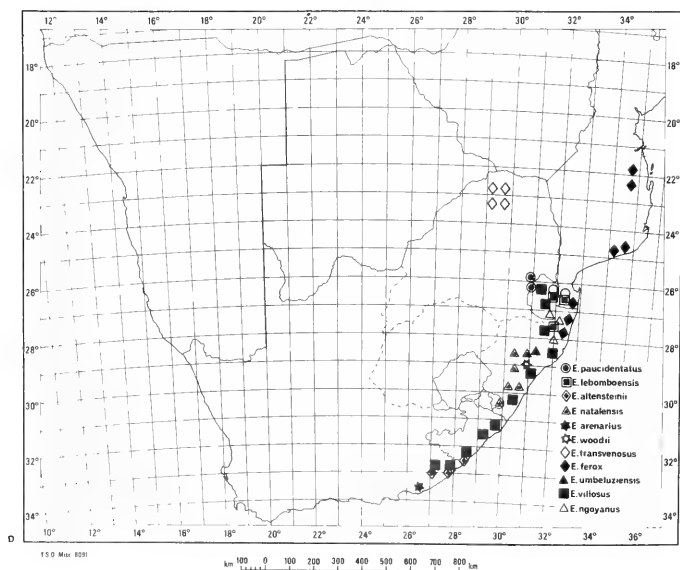
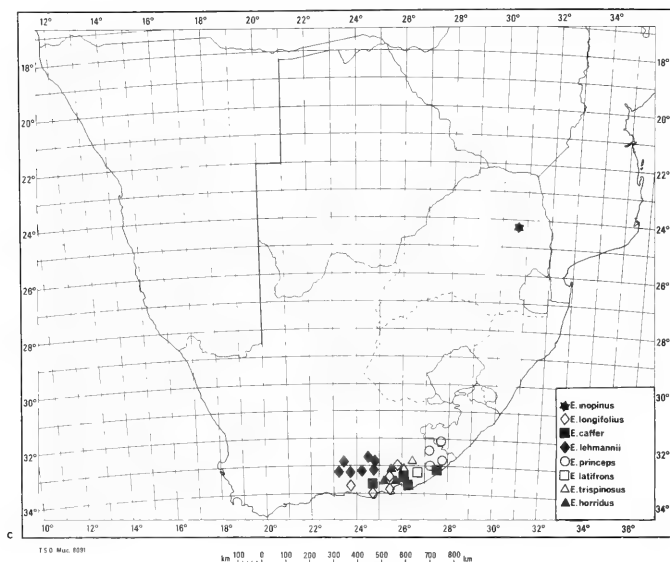


FIG. 2 A-D

Kaarte van Suid-Afrika om die verspreiding van sekere *Encephalartos*-soorte aan te dui.



rye stomas, *E. inopinus* (Fig. 9 D) het twee rye maar by *E. arenarius* (Fig. 14 A) kan daar tot ses en meer rye getel word. Die aantal rye stomas oor die breedte van die pinna getel, kan dus gebruik word om sekere spesies te onderskei. *E. eugene-maraisii* (Fig. 3 A) en *E. cupidus* (Fig. 3 B) se pinnas is egter amfistomaties. Die stomas is ingesink en onderbreek dus nie net die epidermis en kutikula nie maar ook dié weefsels wat onmiddellik onder die epidermis lê.

Greguss (1968) het onder andere die epidermis van die pinnas van 30 verskillende *Encephalartos*-soorte uitwendig ondersoek en hy het porieë wat hy as "rudimentêre stomas" beskryf, by sekere spesies nl. *E. friderici-guilielmi*, *E.*

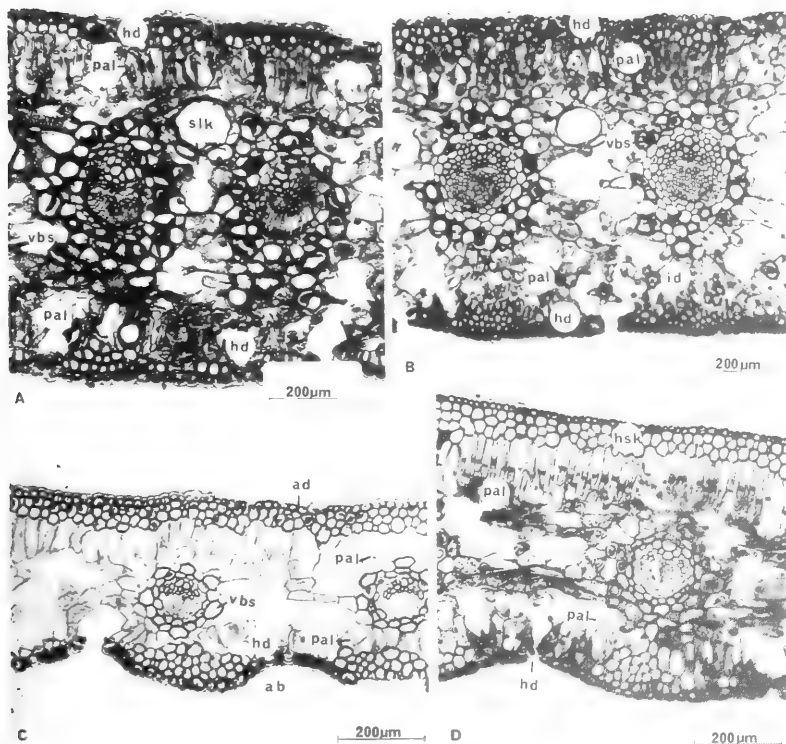


FIG. 3

Gedeeltes van dwarsdeursnee van die pinnas van A. *E. eugene-maraisii*, B. *E. cupidus* C. *E. humilis*, D. *E. laevifolius*, ad adaksiaal, ab abaksiaal, hd stoma, h sk hipodermale sklerenchiem, id idioblaste, pal palissade, slk slymkanaal, vbs vaatbondelskede (Preparate A. 35931P; B. 36975P; C. 37237P; D. 36967P.)

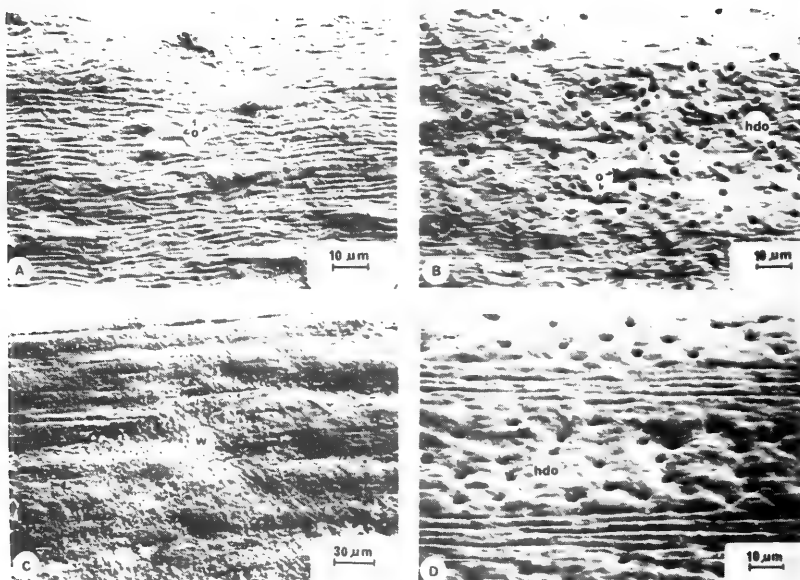


FIG. 4

Elektronmikroskopiese foto's van pinna-oppervlakte van A en B: *E. transvenosus*—A adaksiaal, B abaksiaal, C en D: *E. lehmannii*—C adaksiaal, D abaksiaal, hdo stomatale opening, o opening, w was.

inopinus, *E. lehmannii*, *E. longifolius*, *E. natalensis*, *E. transvenosus* en *E. umbeluziensis* gevind. Hy beweer dat hierdie porieë wat baie min in getal is en slegs op die adaksiale epidermis gevind is, geen sluitselle besit nie en dus nie as ware stomas beskou kan word nie. Jacot Guillarmod en Cross (1972) beskryf soortgelyke openinge by *E. villosus*, *E. trispinosus* en sestion ander *Encephalartos*-spesies wat nie spesifiek genoem word nie, asook by *Stangeria eriopus*, maar spekuleer ook dat die openinge moontlik in verband kan staan met wasafskiedings wat op die blare voorkom.

Tydens hierdie ondersoek is die ab- en adaksiale pinna-oppervlaktes van *E. friderici-guilielmi*, *E. heenanii*, *E. inopinus*, *E. natalensis* en *E. transvenosus* met behulp van 'n aftaselektronmikroskoop ondersoek en openinge wat van stomas verskil is by *E. friderici-guilielmi* (Fig. 5 E), *E. heenanii* (Fig. 5 A, B, C & D) en *E. transvenosus* (Fig. 4 A) waargeneem. As voorbeeld van dié waar die openinge nie gevind is nie, word *E. lehmannii* (Fig. 4 C & D) genoem. Om die oorsprong van die openinge te bepaal is daar na die pinnas van jong blare gekyk. Die pinnas van jong blare is by die meeste soorte dig behaar terwyl dié van ouer

blare glad is. Geen ander openinge behalwe stomas kon egter gevind word nie. Dit is baie duidelik dat die openinge wat deur Jacot Guillarmod & Cross (1972) beskryf is en in Fig. 5 C, D & E aangetoon word, die basale gedeeltes van epidermale hare is. Hulle vertoon soos openinge omdat die dunwandige terminale gedeelte van die hare verdroog en afbreek en daar met die aftaselektronmikroskoop in die lumen van die basale gedeelte ingekyk word. Anders as wat deur Greguss (1968) beskryf word, kom die openinge op die ad- en abaksiale vlakke van die pinnas voor (Fig. 5 A & B).

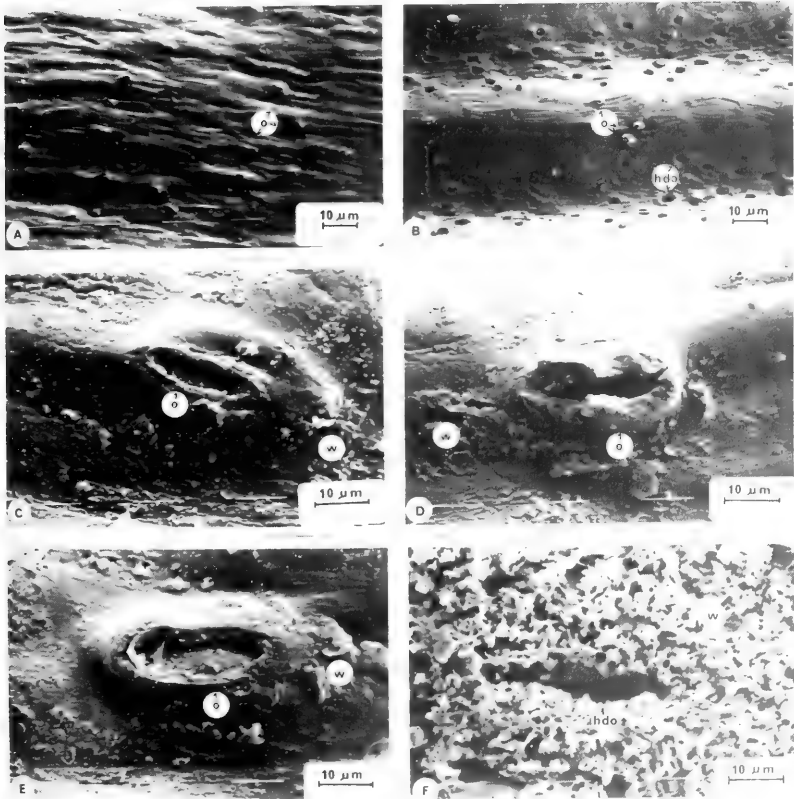


FIG. 5

Elektronmikroskopiese foto's van pinna-oppervlakte van A-D: *E. heenanii*—A en C adaksiaal, B en D abaksiaal, E-F: *E. friderici-guilielmi*—E adaksiaal, F abaksiaal. hdo stomatale-opening, o opening, w was.

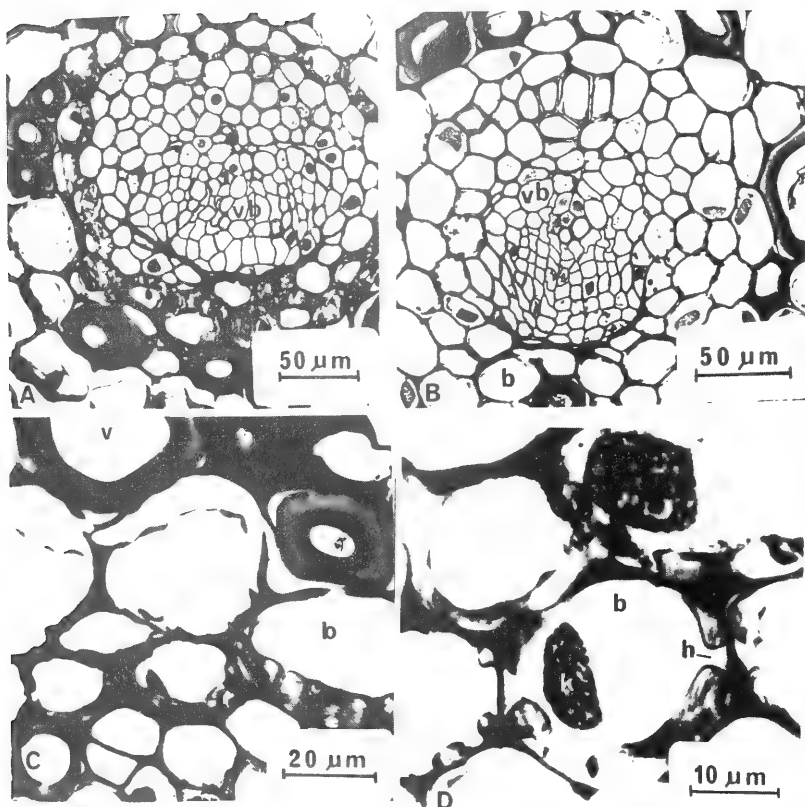


FIG. 6

Dwarsdeursneë van gedeeltes van pinnas van A, C & D: *E. friderici-guilielmi*, B: *E. ferox*, b bondelskedsel, h hofstippel, k selkern, v vesel, vb vaatbondel.

By *E. eugene-maraisii* (Fig. 3 A), *E. cupidus* (Fig. 3 B), *E. altensteinii* (Fig. 14 B) en ander, vorm die ad- en abaksiale vlakke van die pinnas soos in 'n dwarsdeursnee gesien feitlik twee parallelle lyne. Maar by die meeste ander spesies, byvoorbeeld *E. woodii* (Fig. 13 A) en *E. princeps* (Fig. 9 B), is daar 'n effense golwing van die abaksiale vlak van die pinna wat deur lengteverlopende riewe veroorsaak word. By *E. heenanii* (Fig. 8 C) *E. paucidentatus* (Fig. 13 B) en nog 'n aantal ander spesies is daar egter 'n baie sterk golwing van die abaksiale vlak. Die hoogte van die riewe kan dan soos in Fig. 11 A uitgebeeld word in 'n eenvoudige formule as $x = a - b$ uitgedruk word (Fig. 11). Die hoogte van

die rif word dan deur x voorgestel. Die soorte met die hoogste riwwe is *E. cycadifolius* (Fig. 9 A) 93 μm , *E. friderici-guilielmi* (Fig. 8 B) 167–227 μm , *E. heenanii* (Fig. 8 C) 267 μm , *E. latifrons* (Fig. 8 D) 101 μm en *E. paucidentatus* (Fig. 13 B) 257 μm .

Hierdie graad van golwing kan as 'n onderskeidende kenmerk gebruik word. Die kruin van die rif lê teenoor die vaatbondel en in die groewe tussen die riwwe word die huidmondjies aangetref. Hierdie golwing aan die abaksiale vlak van die pinna maak dit maklik om die aantal are van die pinna uitwendig te tel, soos byvoorbeeld by *E. paucidentatus*, sonder om 'n dwarsdeursnee van die pinna te maak. 'n Interessante verskynsel wat slegs by *E. heenanii* (Fig. 8 C) aangetref is, is dat daar op die kruine van sommige van die riwwe een tot twee huidmondjies voorkom. Met behulp van 'n aftaselektronmikroskoop blyk dit ook duidelik dat enkele stomas ylversprei op die kruine van die riwwe voorkom. Hierdie stomas onderbreek dan ook die hipodermale sklerenchiemkappies wat by ander soorte ononderbroke en solied vertoon.

HIPODERMALE SKLERENCHIEM

Hierdie sone kan aan die adaksiale kant van een tot drie ononderbroke lae sklerenchiemselle bevat, byvoorbeeld *E. ngoyanus* (Fig. 12 D) en *E. princeps* (Fig. 9 B), en dit strek van die adaksiale kant om albei rande van die pinna en sluit aan by die abaksiale hipodermale sklerenchiem. Aan die adaksiale kant bestaan die hipodermale sklerenchiem uit vesels terwyl die abaksiale hipodermale sklerenchiem uit sklereïede bestaan. Slegs in die gevalle van *E. cupidus* (Fig. 3 B) en *E. eugene-maraisii* (Fig. 3 A) wat isobilaterale pinnae besit word hierdie sone aan die adaksiale kant deur stomas onderbreek. Alle ander spesies se pinnae is hipostomaties en besit geen stomas aan die adaksiale kant nie en is die sklerenchiemsone aan daardie kant ononderbroke.

Die abaksiale sklerenchiemsone van alle spesies word deur stomas onderbreek. 'n Verdere opvallende verskil tussen die ad- en abaksiale sklerenchiemsone is dat daar aan die abaksiale kant, tussen die vaatbondels en epidermis, sklerenchiemstringe van een tot ses lae diep, wat in dwarsdeursnee soos kappies lyk, gevind word. Die aantal lae sklerenchiemselle wat die string of kappie vorm verskil nie net by verskillende spesies nie maar varieer ook binne die spesies. So byvoorbeeld wissel die aantal lae by *E. cycadifolius* (Fig. 9 A) van drie tot ses, *Encephalartos transvenosus* (Fig. 13 C) en *E. woodii* (Fig. 13 A) se kappies kan uit tot vyf lae bestaan terwyl by die meerderheid van die spesies net drie tot vier lae voorkom.

By *E. ghellinckii* (Fig. 10 D) bestaan die stringe slegs uit een tot twee lae en is tot so 'n mate gereduseer dat daar nie juis van 'n string of kappie gepraat kan word nie. By die soorte waar abaksiale palissadeselle voorkom, word die sklerenchiemstringe gewoonlik van die vaatbondelskede geskei deur 'n laag

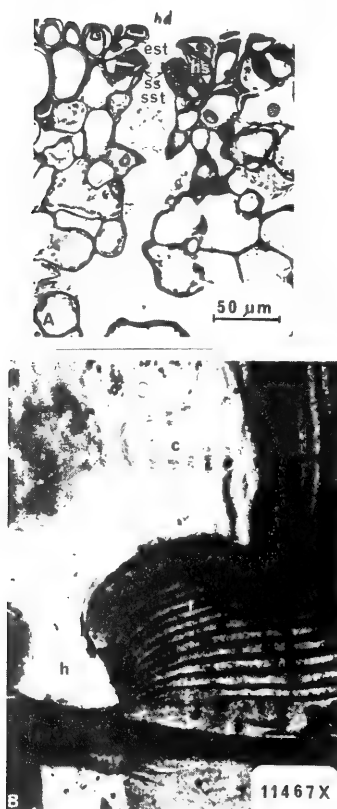


FIG. 7

A. Dwarsdeursee van gedeelte van 'n pinna van *E. ferox*, B. Elektronmikroskopiese foto van 'n bondelskedesel van *E. friderici-guilielmi*, b bondelskedesel, c chloroplaste, est epistomatale holte, h hofstippel, hd stoma, hs hulpsel, k selkern, l lamellae, ss sluitsel, sst substomatale holte.

palissade- sowel as sponsparenchiemselle. Die ander soorte se stringe word slegs deur die sponsparenchiemselle van die vaatbondelskede geskei behalwe by *E. altensteinii* (Fig. 14 B) en 'n paar ander gevalle waar die string soms direk by die vaatbondelskede kan aansluit. Soos reeds gemeld word die sklerenchiemsone onderbreek deur die huidmondjies maar hierby moet gevoeg word dat die hele huidmondjiesone by die meeste spesies totaal vry is van sklerenchiem. By *E. caffer* (Fig. 12 C), *E. lebomboensis* (Fig. 14 D), *E. longifolius* (Fig. 9 C) en *E.*

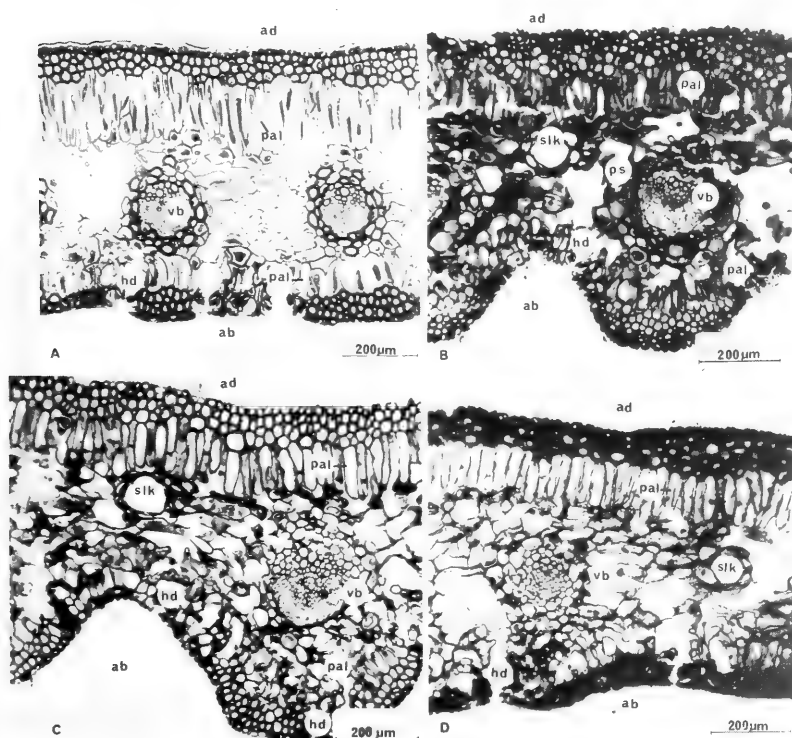


FIG. 8

Gedeeltes van dwarsdeursnee van die pinnae van A. *E. lanatus*, B. *E. friderici-guilielmi*, C. *E. heenanii*, D. *E. latifrons*, ad adaksiaal, ab abaksiaal, hd stoma, pal palissade, slk slymkanaal, ps prominente stippels (kyk Fig. 6), vb vaatbondel. (Prepareate: A. 36961P; B. 37374P; C. 36969P; D. 36948P.)

villosus (Fig. 12 A) word egter klein groepies sklerenchiemsele tussen die stomas gevind.

MESOFIL

Palissadeparenchiem

Die adaksiale palissadeweefsel toon ook heelwat variasie by die verskillende spesies. By *E. lanatus* (Fig. 8 A) kom slegs een palissadesellaag voor terwyl by *E. transvenosus* (Fig. 13 C) en *E. trispinosus* (Fig. 10 C) daar twee tot drie lae voorkom. By die meeste soorte is die selle min of meer baksteenvormig met

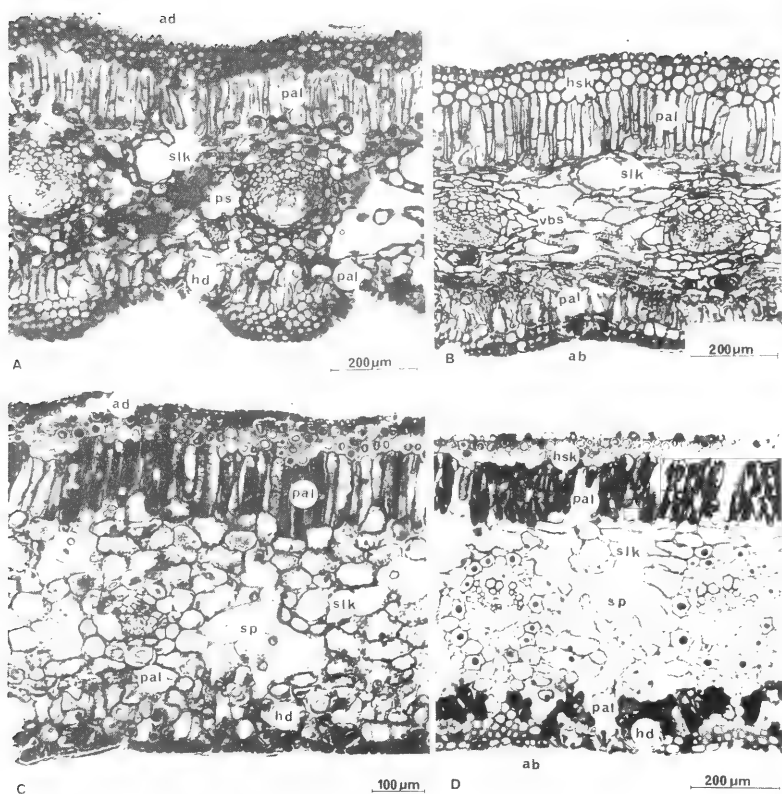


FIG. 9

Gedeeltes van dwarsdeursnee van die pinnas van A. A. *E. cycadifolius*, B. *E. princeps*, C. *E. longifolius*, D. *E. inopinus*, ab abaksiaal, ad adaksiaal, hd stoma, hsk hipodermale sklerenchiem, pal palissade, ps selle met prominente stippels, slk slymkanaal, sp sponsparenchiem, vbs vaatbondelskede. (Preparate: A. 37233P; B. 36940P; C. 35935P; D. 37234P.)

afgeronde hoeke. By *E. lanatus* (Fig. 8 A) is hulle ongeveer twee keer langer as wat hulle breed is maar by *E. transvenosus* (Fig. 13 C) is hulle drie keer langer as breed.

By dertien spesies, naamlik *E. altensteinii* (Fig. 12 B), *E. arenarius* (Fig. 14 A), *E. caffer* (Fig. 12 C), *E. ferox* (Fig. 14 C), *E. ghellinckii* (Fig. 10 D), *E. lebomboensis* (Fig. 14 D), *E. natalensis* (Fig. 13 D), *E. ngoyanus* (Fig. 12 D), *E. paucidentatus* (Fig. 13 B), *E. transvenosus* (Fig. 13 C), *E. umbeluziensis* (Fig. 12

B), *E. villosus* (Fig. 12 A) en *E. woodii* (Fig. 13 A), kom palissadeselle slegs aan die adaksiale kant en stomas aan die abaksiale kant van die pinna's voor. Die pinna's van hierdie spesies is dus suiwer dorsiventraal. Twee spesies, *E. cupidus* (Fig. 3 B) en *E. eugene-maraisii* (Fig. 3 A) is isobilateraal met palissadeselle en stomas aan beide ad- en abaksiale kante.

Die orige dertien spesies word egter ook as dorsiventraal beskou ten spyte van die feit dat hulle ook swak ontwikkelde palissadeweefsel aan die abaksiale kant het, byvoorbeeld *E. inopinus* (Fig. 9 D). Dit kan ook genoem word dat

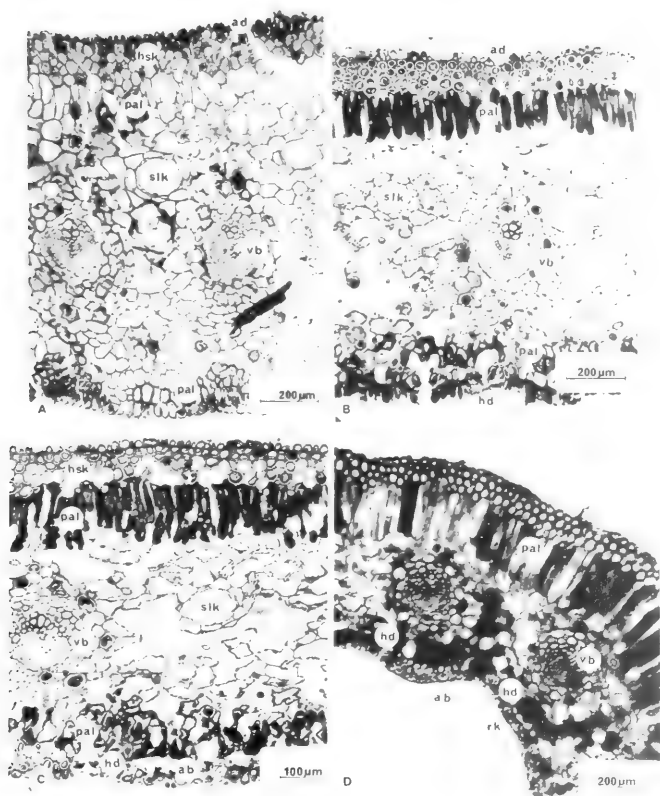


FIG. 10

Gedeeltes van dwarsdeursnee van die pinna's van A. *E. lehmannii*, B. *E. horridus*, C. *E. trispinosus*, D. *E. ghellinckii*, ab abaksiaal, ad adaksiaal, hd stoma, hsk hipodermale sklerenchiem, pal palissade, sp sponsparenchym, rk rande krul om, slk slymkanaal, vb vaatbondel. (Prepare: A. 30974P; B. 36954P; C. 30910P; D. 36943P.)

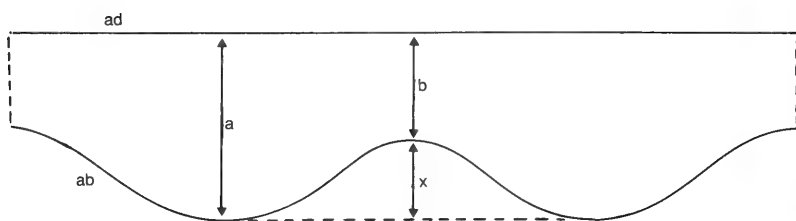


FIG. 11

Diagram van 'n gedeelte van 'n dwarsdeursnee van 'n pinna wat 'n metode illustreer om die rifhoogte van 'n pinna te meet. ab abaksiaal, ad adaksiaal. $X = a - b$

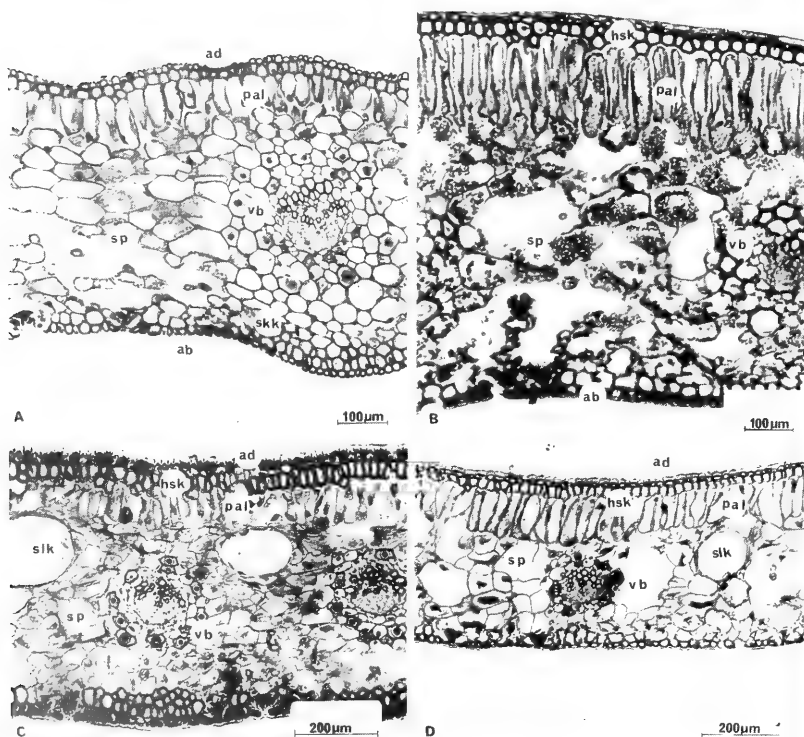


FIG. 12

Gedeeltes van dwarsdeursnee van die pinnas van A. *E. villosus*, B. *E. umbeluziensis*, C. *E. caffer*, D. *E. ngoyanus*, ab abaksiaal, ad adaksiaal, hsk hipodermale sklerenchiem, pal palissade, skk sklerenchiemstring, slk slymkanaal, sp sponsparenchiem, vb vaatbondel. (Preparete: A. 36982P; B. 36949P; C. 36964P; D. 36962P.)

die slymkanale, (indien hulle teenwoordig is) by hierdie dertien spesies in die adaksiale helfte van die pinnae voorkom, behalwe by *E. latifrons* (Fig. 8 D) waar die kanale sentraal geleë is. 'n Verdere aanduiding van die dorsiventrale aard van die pinnae van hierdie spesies is die sklerenchiemstringe, wat slegs in die abaksiale helfte gevind word.

Sponsparenchium

Hierdie weefsel wat uit groot dunwandige parenchiemselle met groot inter-sellulêre lugruimtes bestaan, kan of onreëlmatig van vorm of isodiametries of

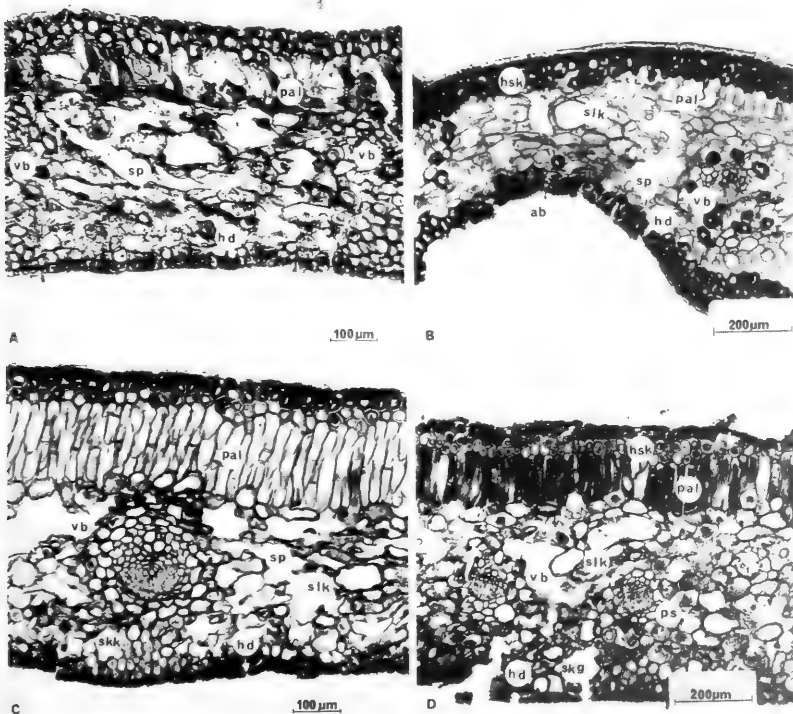


FIG. 13

Gedeeltes van dwarsdeursnee van die pinnae van A. *E. woodii*, B. *E. paucidentatus*, C. *E. transvenosus*, D. *E. natalensis*, ab abaksiaal, ad adaksiaal, hsk hipodermale sklerenchiem, pal palissade, ps selle met prominente stippels, skg sklerenchiemgroep, sp sponsparenchium, skk sklerenchiemstring, vb vaatbondel. (Preparete: A. 35919P; B. 36976P; C. 36970P; D. 36944P.)

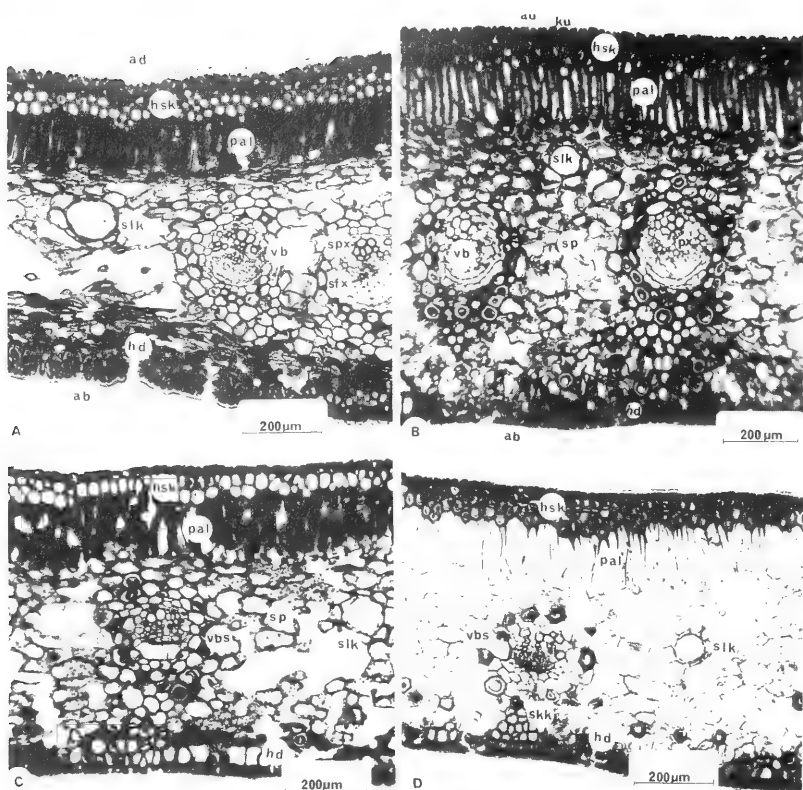


FIG. 14

Gedeeltes van dwarsdeursnee van die pinnas van A. *E. arenarius*, B. *E. altensteinii*, C. *E. ferox*, D. *E. lebomboensis*, ab abaksiaal, ad adaksiaal, hd stoma, hsk hipodermale sklerenchiem, pal palissade, px protoxileem, sfx sentrifugale xileem, ssk sklerenchiem-string, slk slymkanaal, sp sponsparenchym, spx sentripetale xileem, vb vaatbondelskede, vbs vaatbondelskede. (Prepare: A. 30913P; B. 35930P; C. 35931P; D. 36986P.)

opvallend verleng met die lang sye parallel aan die epidermis wees. Tesame met die vaatbondels en kanale vul die weefsel die sentrale deel van die pinna. Kalسيومoksalaatkristalle en dikwandige idioblaste word ook in prepare van sekere spesies aangetref en dikwels word albei in of om die vaatbondelskede gevind.

VAATBONDELS

Hoewel die are digotoom vertak, vertoon die bearing van die pinnas parallel. In dwarsnee is die vaatbondels kollateraál met mesarge primêre xileem. Die protoxileem is min of meer in die middel van die vaatbondel met sentripetale metaxileem adaksiaal en die sentrifugale xileem abaksiaal van die protoxileem geleë. Die sentripetale xileem strek vanaf die protoxileem tot by die adaksiale pool van die vaatbondel. Die floëem lê abaksiaal van die sentrifugale xileem met die protofloëem in die abaksiale pool. Daar moet opgelet word dat die protoxileem by die pinna direk aan beide die sentripetale- en sentrifugale xileem grens sonder 'n parenchiemskede tussenin. In teenstelling hiermee is gevind dat by die petiolus en die blaarbasis, die protoxileem dikwels van die sentripetale- en altyd van die sentrifugale xileem deur parenchiemselle geskei is. By die pinnas is geen fassikulê kambium waargeneem nie en dus kan hier geen sprake van sekondêre vaatweefsel wees nie.

In die vaatbondelskedes wat in die pinnas van al die Suid-Afrikaanse *Encephalartos*-soorte voorkom, is lang vesels met sellulose wande en min, onopvallende stippels aangetref. Lamb (1923) noem hulle "bast fibers" maar aangesien die ontogenie van hierdie vesels in hierdie studie nie nagegaan is nie word hulle slegs vesels genoem. By sommige spesies kom 'n tweede tipe dikwandige bondelskedesel voor. Hierdie selle is min of meer baksteenvormig met gelignifiseerde wande en prominente stippels. Die binneste tangensiale wand is geweldig verdik met duidelike lamellas terwyl die buitenste tangensiale wand baie dunner is. Eenvoudige stippelkanale, hofstippels asook kombinasies van die twee is in die wande aangetref soos in Figure 6 en 7 gesien kan word.

Hierdie eienaardige selle wat enersyds aan 'n endodermis herinner en andersyds ook aan steenselle maar ook nie tipies ooreenkom met enige van die bogenoemde seltipes nie, sal voortaan sklereïedagtige bondelskedeselle genoem word. Hul verspreiding verskil by die verskillende spesies. By *E. friderici-guilielmi*, *E. humilis*, *E. laevifolius* en *E. lanatus* strek dié selle ononderbroke rondom die vaatbondel. By *E. altensteinii* en *E. cycadifolius* ontbreek dit slegs by die adaksiale pool van die vaatbondel en vorm dus 'n gesplete silinder. By *E. arenarius* vorm hierdie selle min of meer 'n oop geut om die floëem en by *E. villosus* is slegs enkeles by die abaksiale pool van sommige vaatbondels waarneembaar. By die ander spesies waar sklereïedagtige bondelskedeselle voorkom, soos *E. longifolius*, word 'n min of meer tussenstadium tussen dié van *E. arenarius* en *E. villosus* aangetref. Ander spesies waar hierdie bondelskedeselle gevind is, is *E. ferox* (Fig. 6 B), *E. ghellinckii*, *E. lebomboensis*, *E. natalensis* en *E. umbeluziensis*. By die orige spesies wat nie hier genoem is nie is geen bondelskedeselle gevind nie.

Tipiese transfusieweefsel soos wat by die meeste gimnospermblare aangetref word, kon nie waargeneem word nie.

SLYMKANALE

In die mesofil, afwisselend met die vaatbondels, word by die meeste spesies groot of klein slymkanale aangetref. In dwarsdeursnee kan die kanale sirkelvormig of ovaal van vorm wees met meestal 'n dunwandige skede waarvan die selle kleiner as die omliggende sponsparenchiemselle is. Die kanale is aan die binnekant met 'n lagie epiteelselle uitgevoer.

Die deursnee van die kanale is by *E. caffer* (Fig. 12 C) ovaalvormig en stem min of meer ooreen met dié van die vaatbondels terwyl dit by *E. inopinus*, *E. altensteinii* (Fig. 14 B), *E. arenarius* (Fig. 14 A), *E. ferox*, *E. lebomboensis* en *E. natalensis* sirkelvormig en kleiner as dié van die vaatbondels is.

By *E. ghellinckii* (Fig. 10 D), *E. humilis* (Fig. 3 C), *E. laevifolius* (Fig. 3 D), *E. lanatus* (Fig. 8 A), *E. umbeluziensis* (Fig. 12 B) en *E. villosus* (Fig. 12 A) is geen kanale waargeneem nie. Dit is interessant dat Lamb (1923) ook geen kanale in die pinnas van *Microcycas* gevind het nie.

By *E. heenanii* (Fig. 8 C), *E. ferox* (Fig. 14 C) en *E. paucidentatus* (Fig. 13 B) is die kanale gewoonlik sentraal, op dieselfde vlak in lyn met die vaatbondels, geleë, maar by *E. altensteinii* (Fig. 14 B), *E. arenarius* (Fig. 14 A), *E. lebomboensis* (Fig. 14 D), *E. natalensis* (Fig. 13 D), *E. ngoyanus* (Fig. 12 D), *E. transvenosus* (Fig. 13 C) en *E. woodii* (Fig. 13 A) kan die kanale sentraal of meer adaksiaal, dit is teenaan die palissadeweefsel in die adaksiale helfte, geleë wees, terwyl hulle by die ander gewoonlik adaksiaal geleë is.

SLEUTEL OM DIE SUID-AFRIKAANSE *ENCEPHALARTOS*-SPESIES VOLGENS DIE ANATOMIESE KENMERKE VAN DIE PINNAS SOOS IN 'N DWARSDEURSNEE GESIEN, TE ONDSKEI

- 1 Pinnas amfistomaties.
 - 2 Sklerenchiemkappie abaksiaal van die vaatbondel vier tot ses lae hoog; idioblaste in interkostale deel van lamina aan abaksiale kant **E. cupidus**
 - 2' Sklerenchiemkappie abaksiaal van die vaatbondel twee tot drie lae hoog; geen idioblaste in interkostale deel van lamina nie **E. eugene-maraisii**
- 1' Pinnas hipostomaties.
 - 3 Palissadeweefsel adaksiaal en abaksiaal.
 - 4 Slymkanale ontbreek.
 - 5 Dikte van lamina minder as 500 μm **E. humilis**
 - 5' Dikte van lamina meer as 550 μm
 - 6 Adaksiale palissadeselle se gemiddelde hoogte minder as 140 μm **E. laevifolius**
 - 6' Adaksiale palissadeselle se gemiddelde hoogte meer as 150 μm **E. lanatus**
 - 4' Slymkanale kom voor.
 - 7 Abaksiale buitelyn sterk gegolf; rifhoogte meer as 90 μm .
 - 8 Abaksiale rifhoogte meer as 150 μm .
 - 9 Vaatbondelskede met ononderbroke ring van sklereïedagtige bondelskedselle **E. friderici-guilielmi**
 - 9' Vaatbondelskede met 'n U-vormige band van sklereïedagtige bondelskedselle **E. heenanii**

- 8' Abaksiale rifhoogte minder as 120 μm .
- 10 Ring van sklereiedagtige bondelskedselle om die vaatbondel wat slegs by adaksiale pool onderbreek is **E. cycadifolius**
- 10' Slegs 'n klein hoeveelheid sklereiede om die floëem van die vaatbondel; geen ring nie **E. latifrons**
- 7' Abaksiale buitelyn reguit of effens gegolf; golfdiepte minder as 50 μm .
- 11 Vaatbondelskede bevat sklereiede **E. longifolius**
- 11' Vaatbondelskede bevat nie sklereiede nie.
- 12 Sklerenchiemkappie abaksiaal van vaatbondel altyd van vaatbondel geskei deur palissade- en sponsparenchiem-selle.
- 13 Abaksiale epidermisselle opvallend kleiner regoor die are as in die interkostale deel.
- 14 Adaksiale palissadeselle opvallend kort; nie hoër as 105 μm nie **E. lehmanii**
- 14' Adaksiale palissadeselle hoër as 120 μm **E. trispinosus**
- 13' Abaksiale epidermisselle regoor are nie verskillend van die in interkostale deel nie **E. princeps**
- 12' Vaatbondels aan abaksiale kant nie altyd van sklerenchiemkappies geskei deur palissade en sponsparenchiemselle nie, soms is dit slegs palissade en soms sluit kappie by vaatbondelskede aan.
- 15 Meestal slegs een laag palissadeselle **E. horridus**
- 15' Meer as een laag palissadeselle **E. inopinus**
- 3' Palissadeselle slegs adaksiaal.
- 16 Abaksiale buitelyn diep gegolf; golfdiepte meer as 200 μm **E. paucidentatus**
- 16' Abaksiale buitelyn nie so diep gegolf nie; golfdiepte minder as 150 μm .
- 17 Slymkanale ontbreek.
- 18 Pinnarande krul opvallend om na abaksiale kant **E. ghellinckii**
- 18' Pinnarande krul nie om na enige kant nie.
- 19 Adaksiale palissadeselle se gemiddelde hoogte meer as 140 μm **E. umbeluziensis**
- 19' Adaksiale palissadeselle se gemiddelde hoogte minder as 100 μm **E. villosus**
- 17' Slymkanale kom voor.
- 20 Drie lae palissadeselle aan adaksiale kant **E. transvenosus**
- 20' Twee of minder lae palissadeselle aan adaksiale kant.
- 21 Slymkanale met dieselfde deursnee of groter as 'n vaatbondel.
- 22 Abaksiale sklerenchiemkappies strek nie tot teenaan die vaatbondelskede nie **E. caffer**
- 22' Abaksiale sklerenchiemstringe strek tot teenaan die vaatbondel.
- 23 Twee tot drie rye huidmondjies in interkostale gedeeltes **E. ngoyanus**
- 23' Tot vyf rye huidmondjies in interkostale gedeeltes **E. woodii**
- 21' Slymkanale met 'n kleiner deursnee as dié van 'n vaatbondel.
- 24 Groepies sklerenchiemselle aan adaksiale kant tussen die huidmondjies.

- 25 Vier tot nege rye huidmondjies in interkostale gedeeltes *E. arenarius*
- 25' Twee tot vier rye huidmondjies in interkostale gedeeltes.
- 26 Sklerenchiemstringe sluit aan by vaatbondelskede.
- 27 Abaksiale hipodermale sklerenchiemselle gemiddeld $27 \times 40 \mu\text{m}$ in DS. *E. ferox*
- 27' Abaksiale hipodermale sklerenchiemselle gemiddeld $20 \times 27 \mu\text{m}$ in DS. *E. lebomboensis*
- 26 Sklerenchiemstringe sluit nie by vaatbondelskede aan nie *E. natalensis*
- 24 Groepies sklerenchiemselle aan adaksiale kant tussen die huidmondjies ontbreek *E. altensteinii*

BESPREKING

In hierdie ondersoek is na verskillende anatomiese kenmerke van pinnas gekyk. Dit blyk dat die verspreiding van die chlorenchiem en stomas, die uitbeelding van die sklerenchiemvesels, die slymkanale en die bondelskedeselle die belangrikste kenmerke is wat gebruik kan word om die ondersoekte soorte te groepeer en 'n sleutel op te stel vir die uitkenning van die verskillende spesies.

Daar is duidelike korrelasie in die verspreiding van die palissadeselle en die aanwesigheid van stomas en hiervolgens kan die verskillende spesies in groepe verdeel word. *Encephalartos eugene-maraisii* en *E. cupidus* het amfistomatiese pinnas en palissadeweefsel kom aan beide ad- en abaksiale kante van die pinna voor. Nie een van die ander spesies besit goed ontwikkelde abaksiale palissadeweefsel nie—die palissadeselle ontbreek aan die abaksiale kant of is altyd korter, kleiner en ook minder in getal as dié aan die adaksiale kant. Daarby kom stomas nie by enige van die ander spesies in die adaksiale epidermis voor nie.

Die volgende groep wat uit dertien spesies bestaan het hipostomatiese pinnas met swak ontwikkelde abaksiale palissadeparenchiem: *E. cycadifolius*, *E. friderici-guilielmi*, *E. humilis*, *E. laevifolius*, *E. lanatus*, *E. heenanii*, *E. inopinus*, *E. latifrons*, *E. princeps*, *E. longifolius*, *E. lehmannii*, *E. horridus* en *E. trispinosus*. Hulle het almal blou-groen blare en kan wat hul verspreiding betref, in twee sub-groepe verdeel word. Die vyf eersgenoemde spesies, kortliks aangedui as die *E. humilis*-groep, word onderskei deur hulle uiters smal pinnas (3–7 mm) en hulle kom op hoogliggende suurgasveld (Acocks, 1975) voor, byvoorbeeld Middelburg, Transvaal, Kaapschehoop en hoër dele in die omgewing van Cathcart (Fig. 2 A-D). Wat verspreiding betref moet *E. heenanii* (berge by Barberton) en *E. inopinus* (Blyderivierpoort) ook by die *E. humilis*-groep gevoeg word omdat beide ook in die suurgasveld voorkom. Die ander spesies naamlik *E. latifrons*, *E. princeps*, *E. lehmannii*, *E. horridus* en *E. trispinosus* het breër

pinna's (10–15 mm) met 'n dieper blou-groen kleur en hulle kom in die droë Oos-Kaapse valleibosveld en noorsveld voor. *Encephalartos longifolius* wat anatomies ook by hierdie groep ingesluit is het egter groen blare en val, wat verspreiding betref, ook nie in die Karoo-noorsveld nie. Dié soort kom voor in die vogtiger gebiede van die Kaapse ooskus naby Port Elizabeth en behoort dus wat verspreiding betref, tuis by dié groep met die meer mesofitiese kenmerke.

Die volgende groep bestaan ook uit dertien spesies. Hulle besit tipiese dorsiventrals, hipostomatiese pinna's met slegs adaksiale palissadeselle. Hulle het donkergroen pinna's en toon ook meer mesofitiese kenmerke soos breë pinna's en meer huidmondjies. Hierdie kenmerke korreleer goed met hul verspreiding. Met een enkele uitsondering na, naamlik *E. ghellinckii*, kom hierdie groep in die warmer, vogtiger gebiede wat strek van Mosambiek deur Natal en dele van die Kaapse ooskus voor en bestaan uit die volgende spesies: *E. paucidentatus*, *E. lebomboensis*, *E. transvenosus*, *E. villosus*, *E. umbeluziensis*, *E. ngoyanus*, *E. woodii*, *E. ferox*, *E. natalensis*, *E. caffer*, *E. arenarius*, *E. altensteinii* en *E. ghellinckii*. Laasgenoemde spesie hoort wat sy verspreiding betref by die *E. humilis*-groep.

Met hierdie korrelasie van anatomiese kenmerke en verspreiding wil dit dus voorkom of hier van twee ontwikkelingslyne sprake kan wees. Hierdie "lyne" begin by 'n hipotetiese gemeenskaplike voorouer van al die Suid-Afrikaanse *Encephalartos*-soorte waaruit albei ontwikkelingslyne dan voortgespruit het. Die een "lyn" eindig in die *E. humilis*-groep met hul smal pinna's, aanpassings by 'n vogtiger kouer omgewing, wat in die hoogliggende suurgrasvelde versprei is. Die ander "lyn" loop deur die meer mesofitiese groep met hul donkergroen blare, egte dorsiventrals pinna's en verspreiding in die warmer, vogtiger gebiede. Hierop volg dié groep met die blou-groen blare, breë hipostomatiese pinna's met swak ontwikkelde abaksiale palissadeselle wat in die droë Karoo-noorsveld sy verspreiding vind. Die eindpunt van hierdie "lyn" word gevind in die klein groepie met amfistomatiese isobilaterale pinna's wat uit *E. eugene-maraisii* en *E. cupidus* bestaan. *E. cupidus* se verspreiding is beperk tot 'n klein gebied in die Blyderivier-natuurreservaat terwyl *E. eugene-maraisii* 'n wye verspreiding het. Hierdie spesie kom voor in die droë laeveldse bosveld by Mica in die ooste, in die suurveld op die Wolkberg, in die Krokodilriviervallei en in die Waterberge weswaarts tot by Thabazimbi (Fig. 2). Dit wil dus voorkom asof *E. eugene-maraisii* met hierdie groot verspreiding en aanpassings die meer resente van die spesies kan wees.

By *E. humilis*, *E. laevifolius*, *E. lanatus*, *E. ghellinckii*, *E. umbeluziensis* en *E. villosus* is geen slymkanale in die pinna's gevind nie. By alle ander spesies kom slymkanale afwisselend met die vaatbondels voor. Eersgenoemde vier spesies val onder die *E. humilis*-groep insover dit die verspreiding betref en laasgenoemde twee spesies hoort tuis onder dié groep met die meer subtropiese verspreiding. By al die spesies word vesels in die vaatbondelskedes aangetref. Maar

sklereïedagtige bondelskedeselle is slegs by die volgende spesies in die vaatbondelskedes van pinnas waargeneem: die *E. humilis*-groep, *E. altensteinii*, *E. arenarius*, *E. ferox*, *E. heenanii*, *E. latifrons*, *E. lebomboensis*, *E. longifolius*, *E. natalensis*, *E. umbeluziensis* en *E. villosus* (Fig. 6 A-C).

Sklereïedagtige bondelskedeselle word egter ook in die petiolusse van die *E. humilis*-groep, *E. heenanii*, *E. longifolius*, *E. princeps*, *E. latifrons*, *E. lehmannii*, *E. transvenosus* en *E. trispinosus* gevind. *Encephalartos heenanii* se habitatsvereistes is min of meer dieselfde as dié van die *E. humilis*-groep. Behalwe *E. transvenosus*, *E. umbeluziensis*, *E. villosus*, *E. ferox* en *E. arenarius* wat onder die groenblariges met 'n meer tropiese verspreidingsgebied ressorteer, val al die ander onder dié groep wat in die droë Oos-Kaapse valleibosveld en -noorsveld voorkom. Al die spesies waar sklereïedagtige bondelskedeselle ontbreek val òf in die groep met die breë dorsiventrale pinnas en die meer tropiese verspreidingsgebied òf in die groep met die isobilaterale pinnas met die wye oos-wes verspreiding.

Esau (1965) maak die stelling dat "transfusion tissue is of universal occurrence in the gymnosperms". Brashier (1968) maak melding van 'n transfusieweefsel om die vaatbondel van *Encephalartos*. Van der Schijff en Robbertse (1975) verwys ook na transfusieselle tussen die xileem en die bondelskedeselle van *Stangeria* en *E. laevifolius*. In hierdie ondersoek is daar egter tevergeefs gesoek na tipiese transfusieweefsel. Wat wel gevind is, is sklereïedagtige bondelskedeselle met hofstippels en eenvoudige stippelkanale. As gevolg van die aanwesigheid van hofstippels of hofstippelagtige stippelkanale in die wand van die vaatbondelskedeselle, is dit waarskynlik hierdie selle wat deur genoemde outeurs as transfusieweefsel beskou is. 'n Belangrike waarneming wat tydens hierdie ondersoek gedoen is, is die feit dat die selle lewend is soos die kern en die chloroplaste duidelik aantoon (Fig. 6 D en 7 B).

Greguss (1968) beskryf porieë wat hy op die adaksiale epidermis van die pinnas gevind het as "rudimentêre huidmondjies". Jacot Guillarmod en Cross (1972) het ook soortgelyke openinge op die adaksiale epidermis van sekere *Encephalartos*-spesies beskryf en gesinspeel dat hulle in verband kan staan met wasafskieding. Oppervlakstudies wat gemaak is met behulp van 'n aftaselektronmikroskoop het ook "openinge" getoon maar hierdie "openinge" was die holtes wat nagelaat is deur die basale sel van afgebreekte trigome soos duidelik in Figure 5 C, D & E gesien kan word.

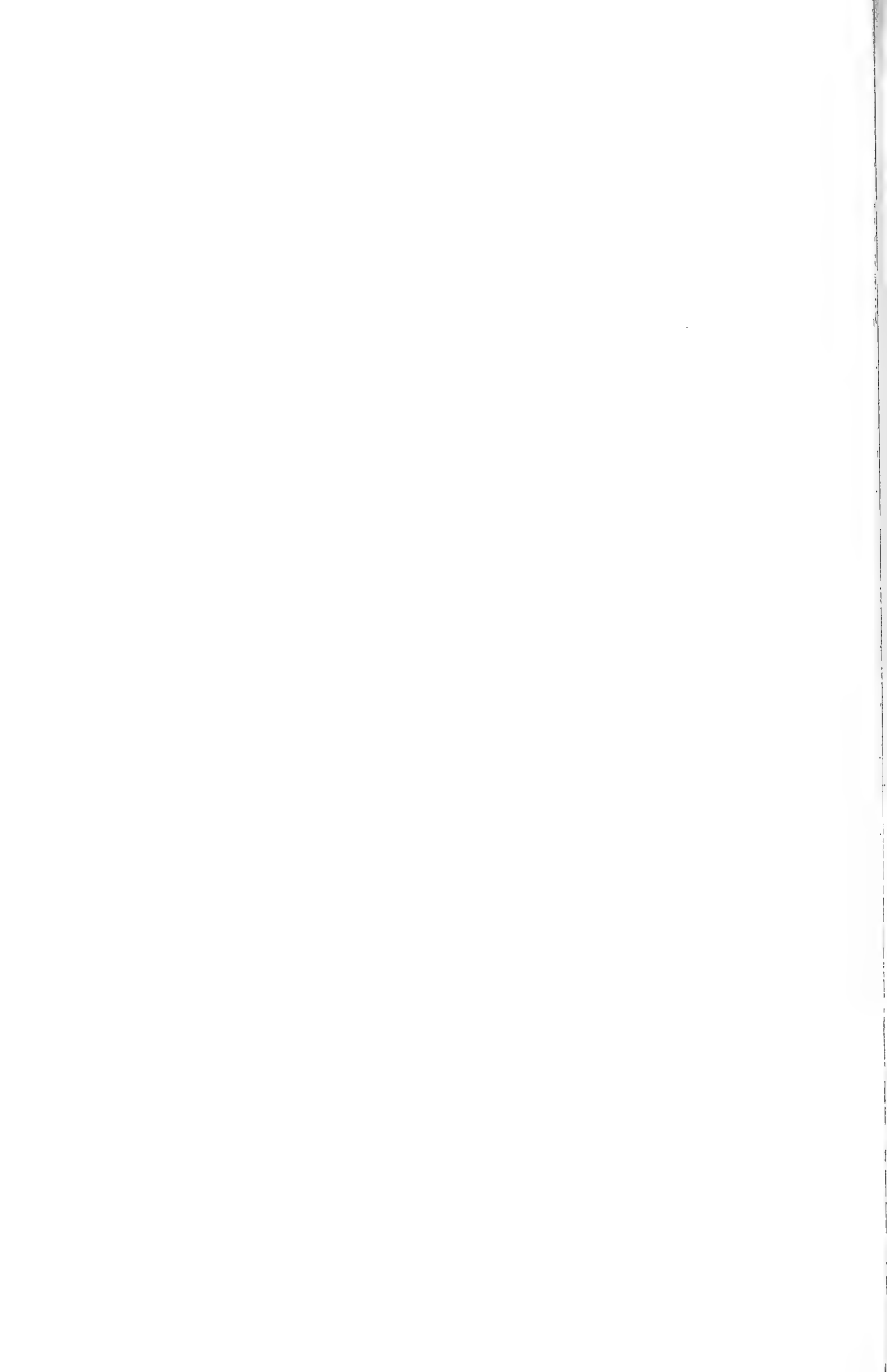
Uit die ondersoek is dit duidelik dat die anatomie van die pinnas van die Suid-Afrikaanse *Encephalartos*-soorte wel tot so 'n mate van mekaar verskil dat hul op grond van hierdie eienskappe van mekaar onderskei kan word.

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SENSITIVE DENDROMETERS FOR CONTEMPORARY RESEARCH. A CRITICAL EVALUATION OF STRAIN GAUGE DENDROMETERS

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ABSTRACT

The design and construction of very sensitive dendrometers using electrical resistance strain gauges is described. A number of circuits that can be used are discussed. The manner in which the sensors have to be attached to the plants is explicitly described, with information about necessary precautions being added.

Examples of the use of the instrument are given, showing their versatility, sensitivity and speed of response.

UITTREKSEL

**SENSITIEWE DENDROMETERS VIR EIETJDSE NAVORSING. 'N KRITIESE
EVALUASIE VAN SPANNINGSMETERS VIR BOOM-METING**

Die ontwerp en konstruksie van uiters sensitiewe dendrometers gebaseer op elektriese spanningsmeters word beskryf. Verskeie moontlike stroombane word bespreek. Die koppeling van die sensors ten opsigte van die plant is duidelik uiteengesit asook inligting rakende die nodige voorsorgmaatreëls wat geneem moet word.

Voorbeelde wat die gebruik van die instrumente, aanpasbaarheid, sensitiwiteit en reaksie tempo illustreer word ingesluit.

INTRODUCTION

There has been a long-standing need for a simple, continuous, non-destructive method for measuring the responses of plants to environmental variables. The daily stem contractions of woody plants, resulting from transpirational losses through the leaves, are well known. Attempts have been made to evaluate the relationship between these contractions and variations in temperature, light, relative humidity, and other environmental parameters (Holmes & Shim, 1968; Jordan & Ritchie, 1971; Klepper *et al.*, 1971; Namken *et al.*, 1969; Splinter, 1967, 1969; Stansell *et al.*, 1973; Turner & Waggoner, 1968; Zaerr, 1971). To satisfactorily evaluate these relationships, accurate and quick measurements of stem size must be made. To do so requires reliable and sensitive dendrometers and dendrographs. This paper describes the design and use of an electrical resistance strain-gauge technique for making such dendrographic measurements.

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Several investigators (Holmes & Shim, 1968; Jordan & Ritchie, 1971; Phipps & Gilbert, 1960) have reported diurnal fluctuations in stem diameter of up to 0.25 mm under high transpiration conditions. Smaller contractions of one-tenth this value are common. It is possible to measure these differences with calipers (Holmes & Shim, 1968), but this is discontinuous and insensitive. Phipps and Gilbert (1960) and Impens and Schalck (1965) used instruments that were far more sensitive but had to be bolted into the heartwood of the tree. Holmes and Shim (1968) drew attention to the large discrepancies in measurements taken with different dendrometers. In particular, the dendrometers that were bolted into the heartwood over-read, apparently because the drilling of the holes over-stimulated cambial growth. Splinter (1967) introduced linear variable displacement transducers (LVDT) to monitor changes in stem diameter. This resulted in a sensitive quick-responding dendrograph, with a resolution of 0.0025 mm in stem diameter.

A number of workers (Namken *et al.*, 1969; Stansell *et al.*, 1973; Klepper *et al.*, 1971; Jordan & Ritchie, 1971) have used this approach with considerable success. Unfortunately, an LVDT has to be mounted on a relatively large frame for attachment to a plant. It also has to be remounted every 20–30 days. Although the resolution is good for large diameter, it represents a larger part of the measured length as that length decreases. It is therefore, less accurate on smaller plants. Diametral measurements are also made with less accuracy than larger circumferential measurements.

Unfortunately, Splinter (1967) in his original paper discussing LVDTs, states that reliable strain gauge measurements, out-of-doors, are difficult to obtain, due to a number of reasons, including callousing of the stem, bonding creep over long periods of time, and thermal gradients across the measuring bridge. His opinion has apparently been widely accepted as fact, and authors such as Kinerson (1971) repeat these views about the unreliability of strain gauges without presenting any factual data to support the statements. In this paper it will be demonstrated that strain gauges are reliable, even for field studies. When correctly applied and incorporated into suitable circuits, they can be used to give highly accurate and versatile dendrographic data.

Whipple (1977) made a thorough survey of dendrographic methods and tabulated them to compare their performance features. It is clear from his ratings that the electrical resistance strain gauge dendrograph described here is generally superior to older methods in performance as well as convenience. When skillfully applied, this method is nondestructive: i.e., it does not harm the tree or affect its physiological behaviour. It measures "strain" (ϵ), which is the dimensionless ratio of change in length (Δl) to original length (l) ($\epsilon = \Delta l/l$) expressed in "parts per million" (ppm) or "microstrains" ($\mu\epsilon$). A resolution of 10 $\mu\epsilon$ is readily achieved in long-term readings and, with care, a resolution of 5 $\mu\epsilon$ (or under exceptional circumstances, 1 $\mu\epsilon$) can be obtained. Since this is a dimen-

sionless number the resolution is the same for large or small plants whether taken on diameter or on circumference. On the same scale an LVDT would, on a 25 mm tree, resolve only 0.0025/25 or 100 $\mu\epsilon$, which is from 20 to 100 times less than can be achieved with strain gauges.

During nine years of development and testing at the University of Cape Town, Iowa State University, and Michigan Technological University (Schütte, 1970; Schütte & Burger, 1973; Whipple *et al.*, 1976), the strain gauge technique has proved to be highly reliable and easy to use under a wide variety of configurations and in many applications. Only a few elementary precautions are needed to obtain automatic, reliable, and continuous recordings of dendrographic data with a hitherto unattainable sensitivity and rate of response.

INSTRUMENTATION

Strain measurements with electrical resistance gauges is a highly sophisticated and widely used technique in the fields of measurement technology and experimental stress analysis. Strain gauges are today used extensively and imaginatively by engineers to solve many diverse measurement problems. They are, in fact, the active sensing elements in many high quality transducers for measuring pressures, flow rates, displacements, forces, etc. Through correct circuit design and intelligent application of the principles of solid mechanics, a researcher can compensate automatically for most of the effects which he considers to be extraneous to his system. Once the correct configurations and circuits have been established, the resulting measurement system is generally very accurate, rugged, and easy to use. In the light of contemporary technology, it is indeed surprising that they have not found use in the plant sciences as well.

Electrical resistance strain gauges operate on the principle that metal alloys experience a change in resistance when stretched. The alloys used for commercial strain gauges increase their resistance when stretched and decrease it when compressed. Thus, if a thin piece of foil is cemented to a surface and the surface is subsequently strained, the glue will transmit the strain to the foil, and the resultant resistance change will be directly related to the strain on the surface. This change in resistance (ΔR) is measured with a Wheatstone bridge and is related to strain through the relationship:

$$\begin{aligned}\text{Strain } (\epsilon) &= \frac{\text{change in length}}{\text{original length}} \\ &= \left(\frac{\Delta l}{l} \right) = \left(\frac{\Delta R}{R} \right) / S \\ \therefore \frac{\Delta R}{R} &= S \epsilon\end{aligned}$$

where S = the "gauge factor" or sensitivity to strain of the gauge

R = the unstrained resistance of the gauge.

For most commercial gauges, R is either 120 or 350 Ω and S is approximately 2.

Contemporary Wheatstone bridges and associated high quality amplifiers can measure the small changes of resistance which occur when a gauge is stretched and display the results directly as "strain" on any one of the large range of readout instruments. Digital voltmeters, galvanometers, and continuous strip chart recorders are widely used to display the results. The stability of these instruments over long periods of time and a wide range of environmental conditions is excellent so that long-term strains of 5 ppm ($5 \mu\epsilon$) can be read reliably and reproduced accurately. Over short periods, resolutions of $1 \mu\epsilon$ can be achieved. When applied to a circular object such as a tree trunk, the "circumferential" strain would, of course, be the same as the diametral strain. Thus, if a gauge is cemented tangentially to the trunk of a tree, it will read both diametral and circumferential changes to unprecedented accuracies. This data can readily be recorded automatically and continuously without the need for surveillance.

Figure 1 (a) shows an enlarged reproduction of a typical strain gauge. Most of the gauges used in the research described here had a gauge length (A) of 6,35 mm, overall length (C) of 9,53 mm, and overall width (B) of 3,16 mm. Smaller gauges were used on small trees. When both vertical and tangential strains were measured, a combined gauge incorporating two grids normal to each other on the same backing strip was used [Fig. 1 (b)]. The gauges are very thin and flexible and handle much like postage stamps. They cost from R1,50 each and come in many shapes and sizes, as a cursory glance at any catalogue will reveal. The selection of the correct gauge is important for the success of a project.

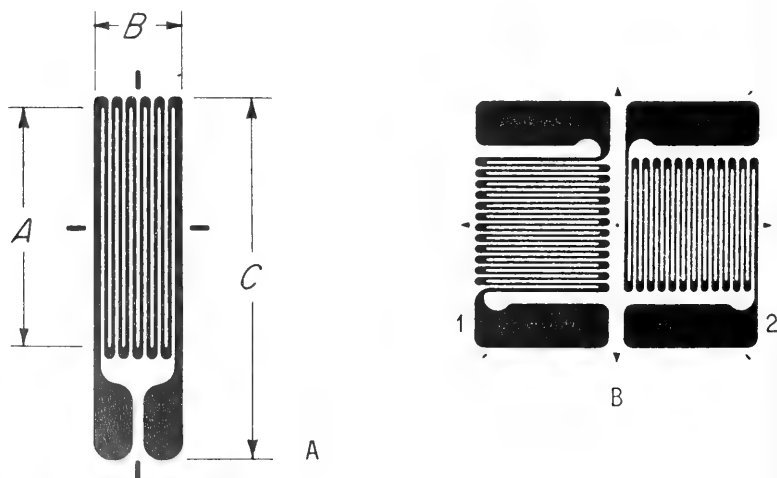


FIG. 1.

Enlarged view of two typical strain-gauge patterns used on trees. A = gauge length; B = gauge width; C = overall grid length.

The ones used by the authors of this work were constantan foil gauges on polyimide backing material. The preferred option was with an encapsulated grid and leads attached. Both 120 Ω and 350 Ω gauges were used, but the former was preferred because of availability and lower cost. The 350 Ω gauges are better, however, because they give larger readout voltages on a Wheatstone bridge and, therefore, require less "sensitivity" from the associated equipment.

POTENTIAL SOURCES OF ERROR

Since strain gauges are so sensitive, it is desirable to use them as accurately as possible. In applying them to trees certain difficulties are encountered which have not been resolved.

The first difficulty is due to changes in environmental temperature: the effect of such changes on the thermal expansion and contraction of the wood and the bark of a tree is very complex. It is not only different in the vertical (axial) and tangential or diametral directions but also varies with the state of hydration of the tree. There is no "typical" coefficient of thermal expansion for the trunk of a living tree. When quasi-equilibrium temperature conditions are disturbed, stable conditions may not be re-established for several hours. In one test the authors imposed a 20 °C cycle for 20 min on the stem of a small (40 mm diameter) tree. The thermal expansion effects caused by this cycle could still be observed 6 hr after normal temperatures had been re-established on the bark.

Despite these anomalous changes, however, the maximum changes can be estimated through carefully set-up measurements (Whipple *et al.*, 1976). They are small compared to the real strain changes that occur over the same time intervals. By careful design of the whole measurement system these errors can be kept to less than 5 % of the strain readings.

It should be pointed out that this error is, and has been, present, to the same or to a larger extent, in all other dendrographic measurements, and it is much harder to do even partial compensation in alternative systems. A good quality strain-gauge system will have smaller errors due to uncompensated thermal expansions than any other dendrograph currently in use.

The second potential source of error derives from the possibility of long-term "creep" in the adhesive layer between the gauge and the tree. The adhesives in general use do not display this tendency when used in regular industrial applications, but their long-term stability when used on live trees has not been fully established. When dealing with living material which shows growth responses to pressures and gravity, it is not easy to design long-term adhesive "creep" tests along traditional engineering lines.

In one investigation tests were run for 24-hr periods during which two opposing vertical gauges were mounted on a trunk of a tree which was bent to give readings of plus and minus 1 000 $\mu\epsilon$ on the tension and compression gauges, respectively. The load was maintained for 24 hr, and the creep was observed.

Long-term physiological adjustments to the bending stem, similar to those alluded to in the discussion on temperature effects, occurred but did not obscure the conclusion that creep, if any, was less than 2 % of the strain reading. Especially clear evidence was obtained from tests that lasted only 8 hr but were performed during the night-time non-transpiring period when the trees did not experience regular physiologically induced strains. *Creep will reduce the strain readings to below their real values.*

The third potential source of error on the use of strain-gauge dendrometers arises when they are being used to measure short-term growth. Since these instruments are very sensitive, they record changes in girth very readily and very rapidly. There is always the temptation to consider these changes in girth as signs of growth. For example, the daily increments observed at the night-time rest condition are not necessarily "growth". These changes may even show negative values for several days simply because the plant suffered a little water stress and was unable to recover fully. Daily increments are not a good measure of growth, unless they are made when the stem is under no water stress. For best results the pattern should be observed over a period of several days.

The fourth source of error results from the possibility that the strain-gauge "backing" material and glue reinforce the bark at the point of application. The bark is then "stiffer" in this region, and the observed strain is less than would have occurred in an unreinforced area. This is especially likely on soft green bark and on very young plants. The authors minimized this error by selecting polyimide backed gauges which are soft, very pliable, and have a modulus lower than most biological materials. The cement was Eastman 910 which, if carefully applied, gives a very thin, high elongation joint which is essentially creep free under most conditions. We do not consider this an important problem in the trees on which we took measurements, but it remains an error that should be guarded against since it is hard to evaluate its effect in any other than an analytical way.

A fifth source of error is the apparent strain that arises when moisture "short circuits" the gauge between the foil grids of a gauge. This leads to small changes in the resistance of the grid which will, of course, appear to be compressive strains. Fully encapsulated polyimide gauges do not have this problem, and in many checks during the night-time "rest period" of our experimental trees we never had any indications that moisture affected the gauges.

The linear strain range for constantan foil gauges is $\pm 5\%$ (50 000 $\mu\epsilon$). If larger strains are expected, annealed constantan (P-alloy) gauges can be used for ranges up to 20 % (200 000 $\mu\epsilon$). For special purposes and long-term growth studies, liquid metal gauges with capabilities of up to 200 % strain are available. Nonlinearity of the gauges is therefore not a problem. Good instruments should also have a linear range. One range should, however, be checked to insure that all voltage readings are linearly related to strain.

TECHNIQUES

The authors have used strain gauges in three basic ways. In the first, the gauges were mounted on a thin metal strap which was wrapped around the tree like a belt. Here, the measurement was the strain on the belt rather than on the tree, and since the belt was much stiffer than the trunk, the output was more precisely a measure of the internal pressure which the expanding and contracting tree applied to the belt than the actual strain in the tree. Signatures of changes were, however, accurate, compensation for temperature was complete, and long-term stability of the adhesive layer was of the highest order. These belts can be moved from tree to tree and are of particular value in field studies on mature trees with rough bark.

The second method is the one described here and is the only real "strain" measurement. The gauges are cemented directly onto the tree as described in a previous paper (Whipple *et al.*, 1976). They read, directly, the tangential strain on the tree. This reference reports on the initial responses observed on a red maple tree (*Acer rubrum*). It also discusses the errors involved and the means by which they may be eliminated. The effects of temperature variations are also considered.

In the third technique, strain gauges are used as active sensing agents on transducers which are clamped to the trees: they measure diametral changes of the stems. The concept is the same as with LVDTs except that temperature compensation can be better, and the device much lighter, more rugged, and has a better resolution.

CIRCUITS

For static or quasi-static strains, such as appear in dendrography, the Wheatstone bridge is the preferred way to measure the small resistance changes that occur in strain gauges. It is generally drawn as shown in Figure 2 with equal resistances in each of the four arms. One, two, or all four of the resistances may be replaced by strain gauges to form a bridge with one, two or four "active" arms. These are known as "quarter", "half" and "full" bridge hookups, respectively. It is customary for the "fixed" resistors to have the same value as the gauges which are being used. Most "bridge networks" provide a stable excitation voltage which should be as low as possible when gauges are used on live tissue. The gauge current will then be low, and the gauge will be able to dissipate the heat without affecting the tissues to which it is glued. One and one-half volts (1.5 V) applied to a 120 Ω bridge will yield a gauge current of only 6.3 milliamps. The heat generated by such a system will be readily dissipated.

If a tree is reasonably axisymmetric, bending and torsional effects can be compensated for by mounting two gauges diametrically opposite to each other on the trunk and hooking them into opposite arms of the bridge. Further details

are given in Holister (1967). It is important to keep all leads between the bridges and gauges of equal length, and to expose them to the same temperature. Failure to do so will cause unbalance of the bridge because of resistance changes in the leads (Holister, 1967).

Single-arm bridges do not compensate for bending nor for errors caused by differential thermal expansion between gauges and the material on which they are mounted. In many investigations these errors are small enough to be neglected when compared to the much larger physiologically induced strains which are being measured. In those cases single-gauge installations are economical and effective. The "three-wire" hookup to the gauge [Fig. 2 (c)] should always be used to equalize the lead resistance included in two adjacent bridge arms.

A four-arm bridge [Fig. 2 (a)] is usually the best arrangement. It is also the most expensive. The preferred configuration is to glue two double gauges [Fig. 1 (b)] diametrically opposite each other onto the trunk of a tree that is straight, round, and axisymmetric in structure. (Trees meeting this requirement may be difficult to find, but reasonably close approximations are adequate for most studies). In each pair one gauge will be horizontal and the other vertical. Bending stresses will then be compressive on one pair and tensile on the other. There will be no normal (extension or compressive) strains in the gauge directions caused by torsion, and each pair will sense identical physiological strains. When wired into the bridge so that the two tangential gauges are in opposite arms and the two vertical gauges in the remaining arms, bending stresses will cause no unbalance while physiological strains will be additive. If the thermal expansions are the same in the vertical and horizontal directions, all four gauges will experience equal strains caused by differential expansion between the tree and gauge, and

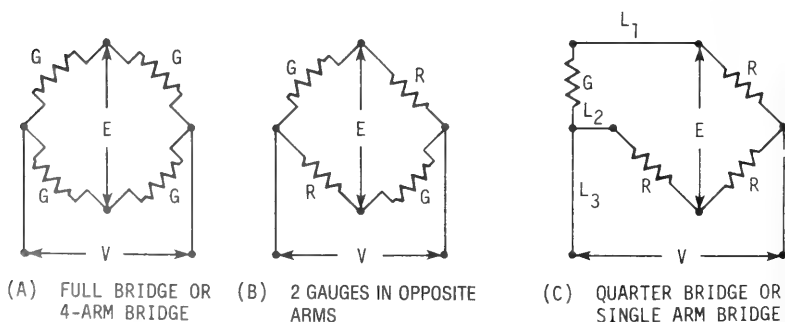


FIG. 2.

Three bridge arrangements used on trees to measure changes in girth. G = active gauge; V = excitation voltage; R = internal balance resistor; E = output as signal voltage; L_1 , L_2 , L_3 = three leads of equal length to single active gauge at a remote position. See text for details of usage.

no unbalance will appear on the bridge. Temperature compensation will be complete. If the further assumption is made that there is no vertical response caused by diurnal cycles or by growth, the vertical gauges will have zero readings from physiological effects. The whole arrangement will be doubly sensitive to tangential changes and insensitive to all the usual errors. Such a system would be ideal.

Unfortunately, live trees sometimes behave in most unusual ways. The authors have observed significant vertical responses in a few isolated instances. In order to separate these responses from the tangential ones, the vertical gauges should be removed from the bridge, which will then have only two gauges in opposite arms. Bending and torsional strains will still cause no unbalance, but differential thermal expansions will introduce errors in the two active gauges. In this setup the strains measured by the two gauges as well as the thermal effects are additive.

This leads to consideration of the quarter bridge with a single active gauge mounted tangentially on the trunk and hooked into the bridge with three wires as shown in Figure 2 (c). This gauge will be fully sensitive to tangential strains and record them directly on the readout instrument with a factor of one because only a single gauge is functional. Strains caused by differential thermal expansion between the gauge alloy and the tree, will, likewise, be recorded with a factor of one and appear as an apparent strain which cannot be separated from the real strain unless the relative coefficients of expansion are known and the bark temperature is simultaneously recorded. In Whipple (1977) and Whipple *et al.*, (1976) these temperature effects have been shown to be much smaller than the physiologically induced strains so that the error is small. How small will depend on the tree species, the state of the tree, and the range of temperature variation. For the maple tree used in Whipple (1977) and Whipple *et al.*, (1976), the largest error was only 2 %

For a straight and axisymmetric trunk, no strains will be recorded due to twisting of the tree. Bending will have a small effect. The cross sensitivity of modern foil gauges (i.e., the sensitivity to strains normal to the gauge length) is usually about +1 %. Thus, a severe bending strain, 100 $\mu\epsilon$ tension, will cause an apparent tangential reading from the source of 1 $\mu\epsilon$. That same tensile strain will, however, cause a compressive strain in the gauge direction due to Poisson's effect of -20 to -30 $\mu\epsilon$. Poisson's ratio for a specific tree may be estimated by comparing the bending strains recorded by a vertical gauge to that of a horizontal gauge. For most trees tested in this programme, the ratio was between -0.2 and -0.3. Oscillations due to wind loads will, therefore, be between 20 % and 30 % of the resulting bending strains.

In a greenhouse such strains are small and may readily be ignored. In the field light breezes seldom introduce strain which is large by comparison with the response readings. If this is troublesome two gauges in opposite ends have to be used for compensation [Fig. 2 (b)]. The temperature error will not be affected

since it will be the same percentage of the reading on each of the gauges. Thus, for indoor studies, the quarter bridge arrangement is often an economical and accurate alternative to more involved systems. The authors have used it extensively in their investigations.

MOUNTING STRAIN GAUGES

Details of one method for mounting gauges are given in Whipple *et al.* (1976). Another method which gives good results for shorter term investigations employs Eastman 910 cement and catalyst (Micromeasurements Instruction Bulletin B127). The procedure is as follows: Lightly sandpaper a small area on a smooth, straight, and round portion of the stem where the gauge is to be mounted. Wipe the area with cotton dipped in acetone or trichlorethylene to temporarily remove grease and dampness. Warm and dry the area by gently blowing hot air onto it with a hairdryer. This provides a slightly warm base for the adhesive which will then cure more quickly. Place the gauge right side up on a clean piece of glass. Overlay it with a 100 mm strip of transparent adhesive tape. The gauge will then stick to the tape. Lift the tape from the glass and transfer the tape and gauge to the tree. Locate the gauge in the correct position and push the tape down to hold the gauge in place. Peel back one end of the tape until the gauge is just off the tree. Apply a very small amount of catalyst to the bark as well as to the back of the gauge and make sure it is dry. Apply a drop of adhesive in the corner between the gauge and the tree and roll the gauge down with the thumb. This spreads the cement evenly and prevents air bubbles from being trapped under the gauge.

The tape should be wide enough so that no cement is squeezed past its edge and comes in contact with the thumb. Apply pressure with the thumb for one minute. Keep applying gentle heat for another 5 min to accelerate the drying process. Solder lead wires to preattached leads and connect to the bridge and readout device. Keep excitation voltage on for 12 hr to maintain the temperature at the glue line. The gauge is now ready for use and will function well for periods of up to eight months. If the gauge is not encapsulated, waterproof the gauge with a thin coating of a suitably flexible agent. The final installation will then have only small reinforcing effects on the bark and will respond very rapidly to strains in the trunk.

Do not attempt to solder directly to the gauge tabs after the gauge has been mounted. The slightest heat from the soldering iron will burn the tree underneath the tab. Callous tissue then forms rapidly and lifts the gauge from the tree. If gauges without preattached leads are used, all lead connections must be made before mounting the gauge.

Eastman 910 cement is single component contact curing cement which is very suitable for polyimide backed gauges. It sets rapidly under thumb pressure but is only fully cured after 12 hr. The performance of the adhesive deteriorates with

time and moisture absorption. The performance of the installation must, therefore, be checked at regular intervals. Solar heating of the gauges must be precluded by covering with cotton or an alumina shield.

The technique for mounting gauges described in Whipple *et al.*, 1976, has better long-term stability but causes more reinforcement. It is best suited to older trees and stiffer bark.

THE INSTRUMENT IN USE

A number of examples of the type of investigation that can be conducted with this equipment are now discussed to show the sensitivity and versatility of this instrument. Details of the experimental investigations and their implications will be treated in other communications.

An individual strain gauge mounted directly onto a tree will read the average strain over the gauge length. It does not read the strains that occur elsewhere around the circumference. If these do not differ significantly from point to point, then a single gauge will do a good job of monitoring the strains in the trunk. If it is required to average over larger lengths, longer gauges are needed or multiple gauges should be mounted in series around the circumference. Foil gauges are generally available up to 50 mm long. Special purpose gauges up to 500 mm long can be obtained.

Example No. 1

A solution for averaging strains over the whole circumference of a tree is to use the thin metal belt discussed before. As an example of the use of belt mounted gauges for field duties, the case of a *Prunus domestica* tree, 107 mm diameter is cited. The *Prunus* tree grew in a sheltered situation in a well-watered and overcrowded garden in the University of Cape Town. The soil was heavy clay. Crowding, soil conditions and restricted light resulted in slow growth and dense wood, but the tree was not deformed in any way. The tree was studied by means of a portable strain bridge and a belt made from bronze shim material 25 mm wide and 0.25 mm thick. A lace-through buckle permitted continuous adjustment so that the belt could be made to fit snugly around the trunk of the tree.

Figure 3 presents the point by point data collected from this over a 28 hr period. The night-time strain is taken as "zero" so that all strains are compressive. The stem fluctuations were almost $80 \mu\epsilon$, which in this case is a diameter change of 0.00860 mm. The stem fluctuations follow the well-known pattern of diurnal stem contractions and are obviously related to environmental parameters such as temperature. Despite the fact that the readings are of an intermittent nature and the belt technique is not the most sensitive form of strain gauge dendrometer, the instrument records considerable detail concerning the short-term variation in the girth of the tree.

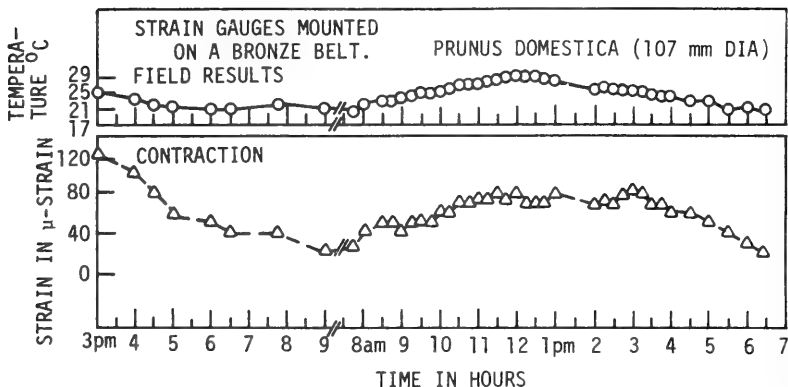


FIG. 3.

Diurnal cycle of ambient temperature and stem contraction data from strain gauges mounted upon a bronze belt around the trunk of a *Prunus domestica* tree, with a stem diameter of 107 mm at 1 m above ground.

Example No. 2

Under the more controlled conditions of a greenhouse, it is possible to utilize the sensitivity and rapid response of the strain-gauge dendrograph more fully. This is well demonstrated by the responses of a drought stricken 1.3 m tall *Acacia cyanophylla* tree grown in a 15-litre pot of clay soil (Fig. 4). Its stem diameter was 18 mm. To investigate the stem responses, a quarter bridge was used and the gauge mounted directly on the stem 126 mm above the soil line. *A. cyanophylla* is adapted to regular water stress, but this plant was subjected to very severe water stress by not watering for eight days. In spite of this it showed a rapid response to light and temperature. Minimum girth (maximum strain) was reached at 11h00 with a contraction of 740 μ e. The rate of change of strain during the preceding hour was very high (230 μ e/hr, representing a diameter contraction of 0.0045 mm). After 11h00 the rate flattened out until the tree was watered at about 13h00.

The influence of light upon the stem contractions can be seen at 09h45. The tree was temporarily shaded from direct sunlight by placing a cloth screen between it and the incoming light. (Lateral light was not excluded.) The result was an immediate reduction in strain (expansion of the trunk) of 125 μ e in 15 min. This very rapid response was completely reversible. When the shade screen was removed, the strain returned to its original level. The magnitude of the *light response* depends upon the time of the day and the physiological state of the plant. It can be measured rapidly and accurately.

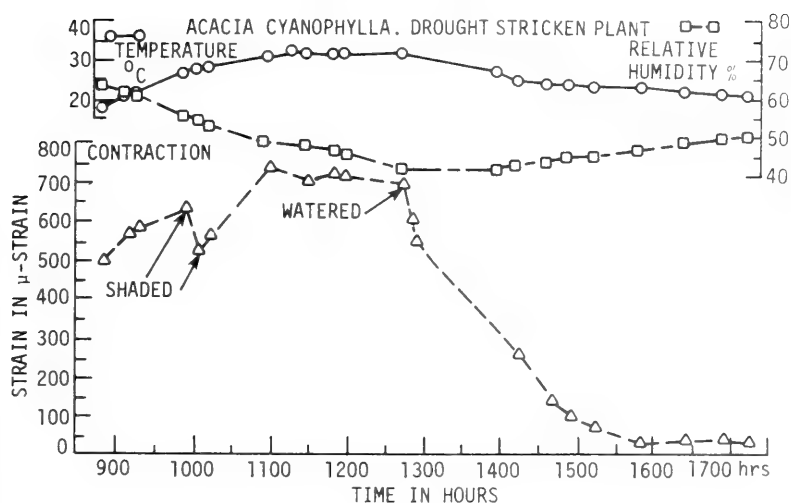


FIG. 4.

Glasshouse studies on pot grown *Acacia cyanophylla*. Strain gauges were mounted directly onto stem. The plant was very severely drought stricken, yet responded to light by contracting its stem. Shading resulted in an immediate response whereby the stem expanded. On re-exposure to light, contraction continued to a maximum at which level it stayed. Response to watering was immediate and very dramatic, concluding at just before 1600 hours.

The relationship between stem behaviour and the hot dry environment can be observed.

The watering response at 13h00 is dramatic. It appeared within 4 sec of the plant being watered. (See Fig. 5 for details of water response.) Expansion of the stem due to watering continued until almost 16h00. The overall recovery was a most impressive $660 \mu\epsilon$ in 3 hr. Although this response is dramatic on the graph, it represents a change of only 0.0117 mm in diameter. The dendrograph measured this effect readily and about instantaneously.

Example No. 3

Continuous recordings give much more versatility to the experimenter, by enabling him to measure lag and response times accurately. The degree of accuracy and sensitivity achievable is demonstrated in Figure 5, where the response to watering in *Populus alba* \times *dentata* was investigated. This plant was grown in a horticultural potting mixture in the greenhouse, and its general strain response to watering was known to be rapid. Upon accurate investigation, it could be shown that the stem completely reversed its daytime pattern of contraction and started to expand within less than 3 sec of water being supplied to the

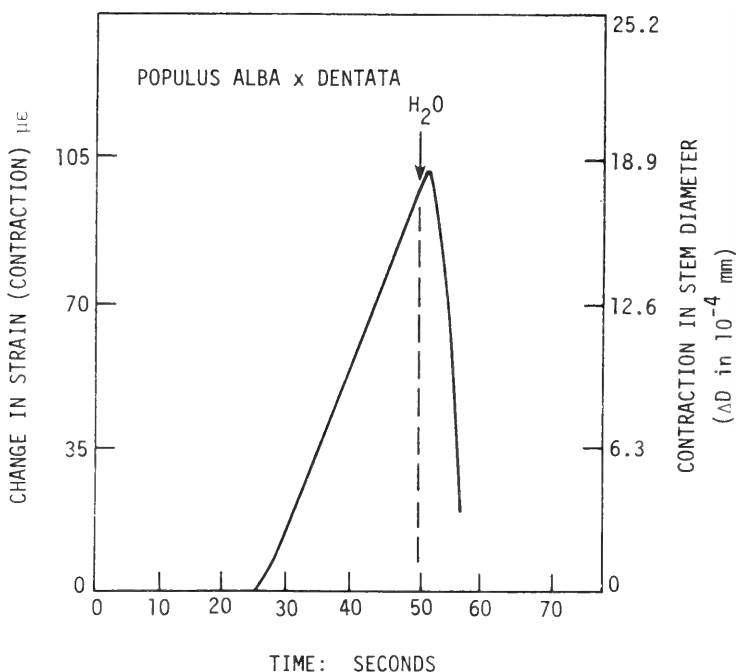


FIG. 5.

Rapidity of watering response: glasshouse grown *Populus alba* \times *dentata* had strain gauges directly mounted on its stem. The stem was contracting steadily, as the recording shows. The plant was watered at the 50 second mark. Within less than 3 seconds of the water making contact with the soil, the entire trunk had ceased to contract and started to expand at a spectacularly rapid rate.

pot. Allowing for the time it took the water to reach the roots, this must be considered an almost instantaneous reversal of strain. In the subsequent 5 sec, the change in strain was $85 \mu\epsilon$. (This is a dimensional change of 15×10^{-4} mm in 5 sec in a stem 18 mm in diameter.) This type of result is reproducible. Its significance will be discussed in a subsequent publication.

Example No. 4

The light reaction is equally amenable to experimental investigation. A small *Populus alba* \times *dentata* was kept in the dark for two days and then moved into deep shade. It was watered regularly to prevent any water deficits developing. It was placed under a bank of Photoflood lamps. The influence of various intensities of light upon the rate of contraction of the stem was studied for periods of

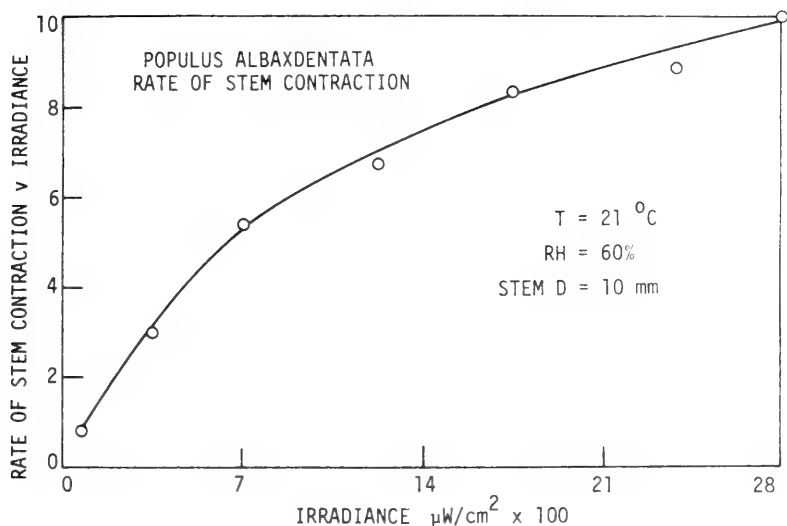


FIG. 6.

A study of the influence of light intensity upon the rate of stem contraction in *Populus alba* \times *dentata* shows that at low light intensities the light is far more efficient per irradiance unit, in bringing about stem contractions, than it is at high intensities. The relationship is predictable.

10 min. During these times the response remained linear. There is a very clear relationship between the irradiance of the light and the stem contraction, as the results in Figure 6 show. The significant response to low light intensities which has been observed in the field and in other investigations, can be readily measured by these techniques, as they are associated with almost instant stem changes.

Example No. 5

Daytime oscillations characterise these dendograms (Fig. 7). The periodicity of the cycles appears to be characteristic of the species and ranges from 20 to 90 min in the plants investigated to date.

At higher sensitivities, other dynamic cycles with periods of less than a minute become evident (Fig. 8). They are particularly interesting because their amplitude and frequency are altered by watering. In Figure 8 the oscillations occur at periods of 30 sec to 90 sec and have an amplitude of about $1 \mu\epsilon$. Once again, these oscillations had no links with environmental or other external sources of "noise". They are quite persistent, and since their characteristics appear to alter with the state of stress of the trees, they may play an important part in studies of water relations.

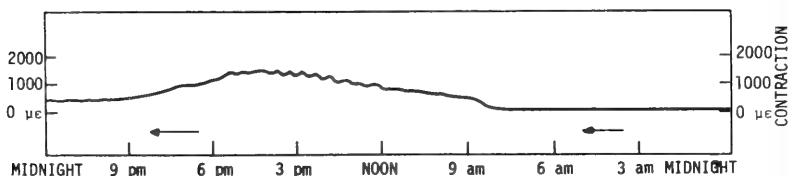


FIG. 7.

Continuous strip chart recording of stem girth for an entire day, showing the endogenous and characteristic oscillations during the daylight period, which are completely absent at night. The oscillations may have other effects superimposed upon them and are not always as clearly evident as in this recording.

Figure 8 is a gymnosperm *Podocarpus latifolius* and Table 1 shows the effect of watering on two species, *Populus* and *Alnus*. Changes in these oscillations are slower to occur than the first response of strain to watering. It may take up to 10 sec to be expressed clearly. While the exact nature of the phenomenon being recorded is unclear, it is compatible with the concept that hydration is altering the volume of the wave conducting tissues and so altering its frequency. There is reason to believe that this type of investigation may be of value in rehydration studies and in studying the path of water conduction in the stem.

There is uncertainty as to whether the small waves recorded in the latter study are similar to, or analogous with, slightly smaller waves of a much slower frequency observed previously in *Podocarpus* which is a gymnosperm and has a different type of anatomical structure.

DISCUSSION

Strain fluctuations vary greatly in magnitude from one species to another, even between trees of the same species but with different growth histories. Holmes and Shim (1968) reported average diurnal fluctuations in Canary Island Pines of 600 $\mu\epsilon$ in summer and 180 $\mu\epsilon$ in winter. The authors of this paper have observed daily fluctuations of around 1 000 $\mu\epsilon$ in a black poplar as well as in *Podocarpus latifolius*, 700 $\mu\epsilon$ in a red maple (Whipple *et al.*, 1976), and up to 6 000 $\mu\epsilon$ in a pot-grown *Populus* hybrid which was under water stress at the time. In cotton plants which are, of course, semi-herbaceous rather than woody, fluctuations of 26 000 $\mu\epsilon$ are not uncommon (Namken *et al.*, 1969). In this context, it is well to note that the light responses first observed by Namken *et al.* (1969) and Stansell *et al.* (1973) in cotton are considerably larger than those in the *Acacia* depicted in Figure 4. In cotton changes of up to 1 400 $\mu\epsilon$ in 5 min have been observed. But the stem girth fluctuations are also proportionately much greater in herbaceous plants than in woody plants. Woody plants with low

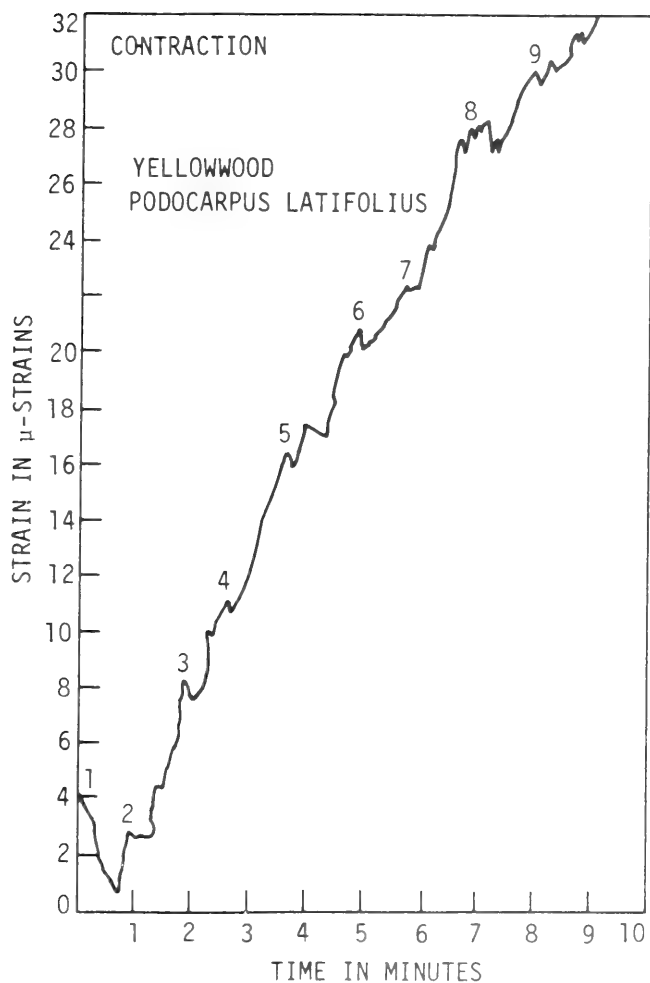


FIG. 8.

Short term, micro-oscillations are characteristic of all plants tested so far. The *Podocarpus latifolius* is a good example although in many plants the frequency will be greater.

TABLE 1.
Influence of Watering upon Micro-oscillations of Tree Stems

Plant	Treatment	Frequency, cycles/min	Amplitude, $\mu\epsilon$	Frequency \times Amplitude
<i>Populus alba</i> \times <i>dentata</i>	Before watering	100	1,75	175
	1 min after watering	256	0,70	179
	20 min after watering	112	1,75	196
<i>Alnus glutinosa</i> L.	Before watering	92	3,75	345
	10 min after watering	128	2,50	320

density woods and soft bark show greater fluctuations than ones with dense wood and compact bark. In all these plants, however, the pattern of the responses to environmental variables is very similar.

The fact that stem strain is such a sensitive index of the behaviour of a tree is of great importance. The strain patterns obtained with strain gauges reveal information about the entire plant, as a system, that is difficult to obtain by other means. Most of the detailed stem variations have not been observed previously. This data is hard to explain at this time because it takes us down to a tissue level that has not been accurately measured in dendrographic observations before. Future research will attempt to answer some of these questions.

CONCLUSIONS

Initial results from the use of strain gauges applied to the trunks of trees lead to the conclusions that:

1. Strain-gauge dendrography is a practical and adaptable technique for investigating water and environmentally related responses in trees.
2. The high degree of precision attainable allows detailed recording of water utilization and stress in trees.
3. The system measures light responses of intact trees.
4. The system is capable of yielding information about little known phenomena such as micropulses in tree stems.
5. Accurate growth measurements are possible and in need of detailed investigation.
6. This basic system is well suited to study water relations in trees. It will be particularly useful for studying water utilization.

ACKNOWLEDGEMENTS

This work was initially financed by a Staff Research Fund Grant from the University of Cape Town. It was further sponsored by the Departments of Forestry, of Engineering Science and Mechanics and the Graduate College of Iowa State University which bodies subsidized the sabbatical leave of one author (K.H.S.) and the costs of these studies. All assistance is gratefully acknowledged.

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 7-9.

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7. **ERIOSPERMUM CAPENSE** (L.) Salter

- CHROMOSOME NUMBER: $2n = 14$ (Figs 1a, b).
ORIGIN OF MATERIAL: Brewelskloof, C.P. (Collection P. L. Perry KG 888/77). Compton herbarium accession no. 119556 (NBG).
METHOD OF PREPARATION: Root tip material. Colchicine pretreatment, Feulgen Acetic orcein staining.
OBSERVATIONS: Chromosomes all acrocentric, with one conspicuous nucleolar pair.

8. **ERIOSPERMUM DREGEI** Schönl.

- CHROMOSOME NUMBER: $2n = 14$ (Figs 2a, b).
ORIGIN OF MATERIAL: Springbokvlakte, C.P. (Collection P. L. Perry 622). Compton herbarium accession no. 119865 (NBG).
METHOD OF PREPARATION: As in 1.
OBSERVATIONS: As in 1.

9. **ERIOSPERMUM PUSTULATUM** Marl. ex Duthie

- CHROMOSOME NUMBER: $2n = 14$ (Figs 3a, b).
ORIGIN OF MATERIAL: Sutherland, C.P. (Collection P. L. Perry 309). Compton herbarium accession no. 119576 (NBG).
METHOD OF PREPARATION: As in 1.
OBSERVATIONS: As in 1.

1a



FIG. 1A.

E. capense, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

1b

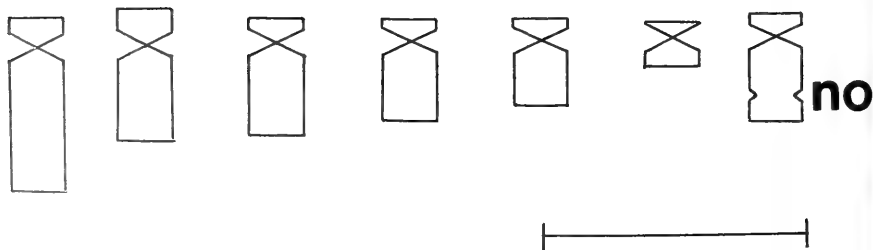


FIG. 1B.

E. capense, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

2a

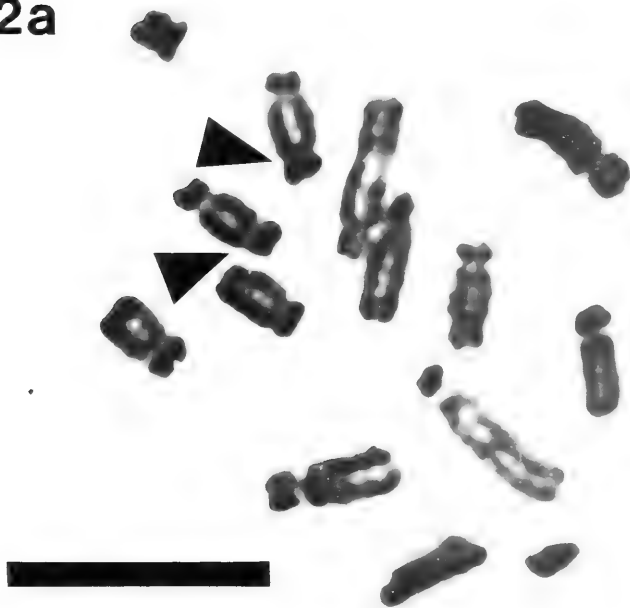


FIG. 2A.

E. dregei, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

2b

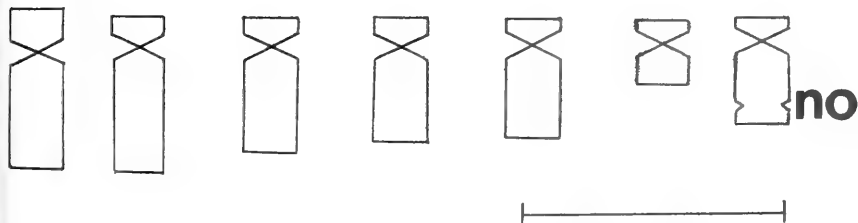


FIG. 2B.

E. dregei, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

3a



FIG. 3A.

E. pustulatum, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

3b

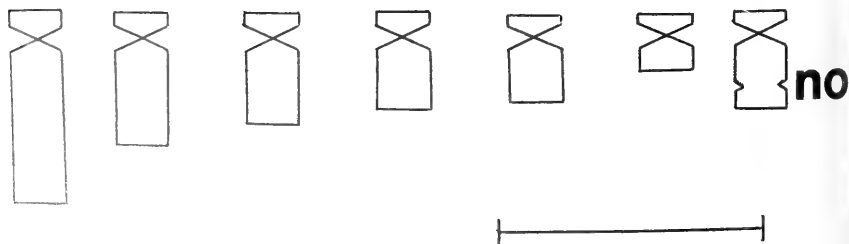


FIG. 3B.

E. pustulatum, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

STUDIES IN OTIOPHORA ZUCC. (RUBIACEAE):

2. A NEW CLASSIFICATION OF THE SOUTHERN AFRICAN TAXA

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ABSTRACT

Six taxa of *Otiophora* occur in and are confined to southern Africa: *O. calycophylla* subsp. *calycophylla* from the Magaliesberg, N. Transvaal and Natal, and *O. calycophylla* subsp. *verdcourtii* (subsp. nov.), endemic to the E. Soutpansberg; *O. cupheoides*, following the Drakensberg escarpment from the E. Transvaal to Swaziland; *O. inyangana* subsp. *inyangana*, widely distributed in the E. Highlands of Zimbabwe (Rhodesia) and neighbouring Mozambique. *O. inyangana* and subsp. *parvifolia* (stat. nov.), a Chimanimani quartzite endemic; *O. lanceolata*, narrowly endemic to the Haroni-Makurupini area.

O. calycophylla subsp. *calycophylla* and *O. calycophylla* subsp. *verdcourtii*, *O. cupheoides*, and *O. inyangana* subsp. *inyangana* have a chromosome number of $n = 17$ and $2n = 34$; pollen measurements indicate that the remaining two taxa are on the same ploidy level.

Investigations into the possible causes of morphological variability of some of the taxa revealed that, at least in *O. cupheoides* and *O. inyangana* subsp. *inyangana*, fire plays an important role; the effect of other environmental factors is also briefly discussed.

UITTREKSEL

STUDIES IN OTIOPHORA ZUCC. (RUBIACEAE):

2. 'N NUWE KLASSIFIKASIE VAN DIE SUIDER AFRIKAANSE TAKSA

Ses taksa van *Otiophora* kom voor in en is beperk tot Suider Afrika: *O. calycophylla* subsp. *calycophylla* vanaf Magaliesberg, N. Transvaal en Natal en *O. calycophylla* subsp. *verdcourtii* (subsp. nov.), endemies aan die Oos-Soutpansberg; *O. cupheoides* op die Drakensberg platorand van O. Transvaal tot Swaziland; *O. inyangana* subsp. *inyangana*, wydverspreid in die Oostelike Hooglande van Zimbabwe (Rhodesië) en naburige Mosambiek, en *O. inyangana* subsp. *parvifolia* (stat. nov.), 'n Chimanimani endemiese op kwartiet; *O. lanceolata*, eng endemies tot die Haroni-Makurupini gebied.

O. calycophylla subsp. *calycophylla* en *O. calycophylla* subsp. *verdcourtii*, *O. cupheoides* en *O. inyangana* subsp. *inyangana* het 'n chromosoomgetal van $n = 17$ en $2n = 34$; beoordeel aan stuifmeelmetings is die oorblywende twee taksa op dieselfde ploiedvlak.

'n Ondersoek na die moontlike oorsake van die morfologiese veranderlikheid van sommige taksa blyk dat, ten minste by *O. cupheoides* en *O. inyangana* subsp. *inyangana*, vuur 'n belangrike rol speel; die invloed van andere omgewingsfaktore word ook kortliks bespreek.

INTRODUCTION

Otiophora Zucc., a genus centred in tropical Africa and also occurring on Madagascar, is represented in southern Africa by several isolated and endemic

taxa¹. Although the genus has been monographed fairly recently (Verdcourt, 1950), particularly in southern Africa a number of taxonomic problems such as the variability of *O. inyangana* N.E.Br. and its taxonomic treatment (Verdcourt, l.c.) or the distinctiveness of *O. calycophylla* (Sond.) Schlecht. & K. Schum. and *O. eupheoides* N.E.Br. (Verdcourt, 1973) has remained unsolved, possibly because the monographer of the genus was not acquainted with the southern African plants in the field and had based his revision on herbarium material. With this in mind, a special attempt was made to undertake an extensive field study.

A new classification of the southern African taxa is presented, based on these field studies and a thorough investigation of the herbarium material available, coupled with karyological investigations and pollen measurements.

MATERIAL AND METHODS

In addition to documentation material brought back by the author from field excursions in South Africa, Swaziland, and Zimbabwe (Rhodesia) (deposited at the herbaria J and/or WU; some duplicates at BR), *herbarium specimens* from the following herbaria were investigated: B, BOL, BR, E, G, GRA, J, K, LISC, MO, NBG, NH, NU, P, PRE, S, SAM, SRGH, STE, W, WU, and Z (abbreviations after *Index Herbariorum*, Holmgren & Keuken, 1974).

For *karyological investigations*, flowers, buds or shoot apices were fixed in the field in 3 parts 95 % alcohol and 1 part HOAc. Preparations were examined using either the conventional squash method (with acetocarmine as stain) or a new method developed by Guerra (1980). Methods/materials for *pollen measurements* are described in Puff (1976).

SEM investigations (Figs 5 and 8) were carried out in a Jeol JSM-T20 Scanning Microscope at the EM Unit, University of the Witwatersrand. Plant parts were fixed in the field in 2.5 % glutaraldehyde in cacodylate buffered sucrose (pH 7.4), then critical point dried and coated with gold-palladium.

The presentation of *distribution records* follows Puff (1978).

KARYOLOGY AND POLLEN MEASUREMENTS

The small size of the chromosomes (c. 0.9–1.3 μ m in metaphase I and II of PMC meioses, and even smaller in somatic mitoses) makes chromosome-morphological studies impossible. No disturbances were observed in mitoses. Meioses of PMCs take place at a very early stage of development of the flowers (the buds are hardly 1 mm long; flowers strongly protandrous). Meiotic irregularities (mainly clumping of chromosomes) were only observed in PMCs of buds

¹ Another species, *O. scabra* Zucc. (subsp. *scabra*), also occurs in southern Africa. This species, not closely allied to the strictly southern African taxa, merely reaches its southern limit of distribution in Zimbabwe (Rhodesia). It is, therefore, only included in the key and distribution map (Fig. 10). For further information on *O. scabra*, see Puff (1981).

developing unusually late (i.e. buds near the apex of already fruiting inflorescences); it is doubtful whether such buds ever develop fully into flowers.

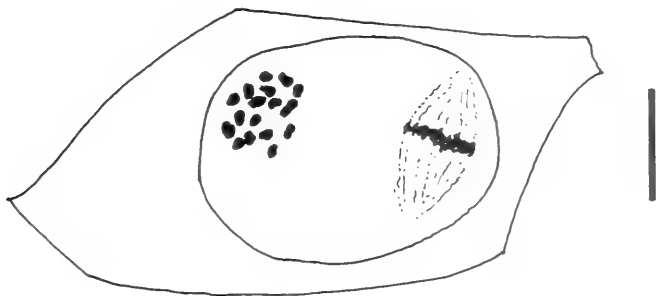


FIG. 1.

Camera lucida drawing of pollen mother cell (metaphase II) of *O. calycophylla* subsp. *verdcourtii* (Puff 791202-2/2). The bar represents 10 μ m.

All taxa investigated karyologically (Table 1) have a chromosome number of $n = 17$ (cf. Fig. 1) and $2n = 34$. This is the same number counted for *O. scabra* subsp. *scabra* (Puff, 1981). The apparent chromosome base number of the genus ($x = 17$) is much-derived and highly unusual in Rubiaceae-Rubioideae. It differs markedly from the base number of African Rubiaceae-Anthospermeae ($x = 11$; Puff, unpublished), to which *Otiophora* was thought to belong¹.

The pollen is fully developed (trinueate) before the buds open. Pollen quality varies: in most flowers (buds) nearly all grains are well developed and abnormal grains (i.e. dead grains not stained red with acetocarmine or exceptionally large grains) are rare; in some the majority of grains are dead (this was sometimes observed in flowers of a single inflorescence, particularly in *O. cupheoides*).

A comparison of average pollen diameters (Fig. 2) of the karyologically known taxa with those of *O. inyangana* subsp. *parvifolia* and *O. lanceolata* leaves little doubt that the latter are on the same ploidy level.

It is interesting to note that the average pollen diameters of the South African species group (*O. calycophylla* and *O. cupheoides*) are clearly bigger than those of the other taxa (compare Fig. 2 a-c and 2 d-f). Because of the relatively small number of samples measured, this difference may not be a true reflection of the situation. The difference, on the other hand, may indicate a much less

¹ A publication dealing with the taxonomic affinities of the genus, Paper 4 of the series "Studies in *Otiophora* Zucc. (Rubiaceae)", is in preparation.

TABLE 1.
Voucher Specimens for Chromosome Counts

	<i>n</i>	<i>2n</i>	Number of individuals investigated
<i>O. calycophylla</i> subsp. <i>calycophylla</i>			
Magaliesberg: ¹			
Puff 790307-2/1 ² (BR, J, WU)	17	34	3
Puff 790706-1/1 (WU)		c.34	2
Northern Transvaal: ¹			
Scholes sub Puff 781218-1/1 (WU)	c.17		1
Puff 791202-3/2 (J)	17	34	4
<i>O. calycophylla</i> subsp. <i>verdcourtii</i>			
Northern Transvaal: ¹			
Puff 791201-1/1 (J)	17		2
Puff 791201-3/2 (J)	17	c.34	2
Puff 791201-4/2 (J)	17		3
Puff 791202-2/2 (J) (Fig. 1)	17		1
<i>O. cupheoides</i>			
Eastern Transvaal: ¹			
Puff 780902-1/1 (BR, J, WU)		34	1
Puff 790211-4/1 (J, WU)	17	34	2
Puff 790704-1/1 (BR, J, WU)	17	34	4
Puff 791208-1/1 (WU)	17		2
Swaziland: ¹			
Puff 770118-3/8 (WU)	17		1
Puff 790225-1/3 (WU)	17	34	2
<i>O. inyangana</i> subsp. <i>inyangana</i>			
Zimbabwe (Rhodesia), Inyanga Distr. ¹ :			
Puff 790124-2/1 (WU)	17		2
Puff 790125-1/2 (WU)	17	c.34	2
Puff 790126-1/1 (WU)	17		3
Zimbabwe (Rhodesia), Umtali Distr. ¹ :			
Puff 790127-2/2 (WU)	17		1
Puff 790128-1/4 (WU)	17	34	3

¹ Exact localities in "Collections".

² The date, on which the voucher specimen was collected and the fixation made, is incorporated in Puff collecting numbers: 790307 = March 7th, 1979; -2/1 = first plant collected in the second locality visited on that day.

close affinity between the two species groups (and between *O. cupheoides* and *O. inyangana* in particular) than the morphological resemblances lead us to believe.

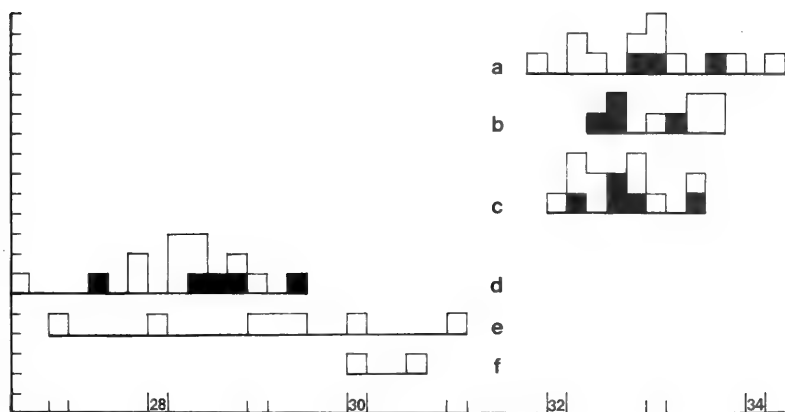


FIG. 2.

Average pollen diameters in μm of *O. calycophylla* subsp. *calycophylla* (a) and subsp. *verdcourtii* (b), *O. cupheoides* (c), *O. inyangana* subsp. *inyangana* (d) and subsp. *parvifolia* (e), and *O. lanceolata* (f). Black: individuals investigated karyologically; vertical scale: no. of individuals.

VARIABILITY

All southern African taxa of *Otiophora* show considerable variation in vegetative and, to a certain extent, floral and inflorescence characters. Characters commonly affected by this variability are growth habit (stems erect, sprawling or straggling, or stems \pm prostrate and much-branched, giving rise to cushions or mats), hairiness, spacing and arrangement of the leaves (decussate or whorled), leaf size, shape and texture, length of fruiting inflorescence, and corolla tube lengths.

To determine the possible cause(s) of this variability and the extent of variation, considerable time was spent in the field analyzing populations. In addition to ecological records, collections were made of a representative number of individuals showing the whole range of variation within a population for further investigations in the laboratory. For each population, this was supplemented by cytological and morphological/anatomical fixations of a few selected plants.

The Influence of Fire

It became obvious from field studies, that in *O. cupheoides* and *O. inyangana* subsp. *inyangana* fire must be one of the major causes of some of the morphological variability displayed by the populations investigated.

For *O. cupheoides*, I would like to demonstrate the effect of fire using as an example a population occurring on the summit of Pypkop (Woodbush Forest Reserve, Eastern Transvaal; Puff 790211-4/1).

The population, consisting of approximately 75 to 100 individuals and occupying an area of c. 30×50 m, was associated with rocky outcrops. The plants grew in cracks of rocks or in depressions of flat rock slabs where a certain amount of soil could collect (usually associated with *Androcymbium* sp. and *Selaginella dregei*), or at the base of rocks at the rock/adjacent grassland boundary. Judging from fairly "fresh" blackened dead stems of various grassland species, the grassland must have been burnt recently (a few months ago?). The considerable variation displayed by the individual plants could very clearly be correlated with exposure/non exposure to fire.



FIG. 3.

A cushion of *O. cupheoides* from a "fire proof" habitat (population Pypkop, Puff 790211-4/1). The bar represents 100 mm.

While plants from clearly "fire proof" habitats, such as plants growing in the middle of large rock slabs (several metres away from the adjacent grassland) or on top of tall boulders, invariably formed dense cushions or mats (Figs 3 and 4b; roughly 50 % of the individuals of the population), recently burnt plants from the rock/grassland boundary were characterized by having \pm erect, long and unbranched stems arising from a woody base (Fig. 4a; roughly 30 % of the individuals of the population).

Plants from habitats which apparently are not always, but sometimes reached by fire (i.e. growing nearer to the grassy areas and, therefore, not completely out of reach of particularly strong fires) were morphologically intermediate between the above extremes (roughly 20 % of the plants).



FIG. 4.

Individuals of *O. cupheoides* from a habitat (a) exposed to, and (b) protected from fire (population Pypkop, Puff 790211-411); b is a portion of the cushion pictured in Fig. 3. a and b: $\times \frac{1}{2}$. Explanations in the text.

Table 2, listing the differences between the two extremes, i.e. individuals clearly exposed to fire and individuals clearly protected from fire, shows that the fire-induced variability largely involves vegetative characters. Variation in the fertile region, length of the inflorescence (i.e. length of the internodes between paired flowers) and size and hairiness of the enlarged, foliaceous calyx lobe, is coupled with the variability in the vegetative region: more elongated inflorescences are associated with longer internodes in the vegetative zone, larger and hairier foliaceous calyx lobes with larger, hairier mid-stem leaves.

Other floral characters such as corolla tube length (4–7 mm) and width (0,3–0,5 mm at the base and 1–1,5 mm below the throat), and corolla lobe size (3–4,3 \times 0,6–1 mm), and to a lesser extent filament and style length, were also found to vary within the population, but this variation was not correlated with exposure/non exposure to fire and almost certainly is purely genetic.

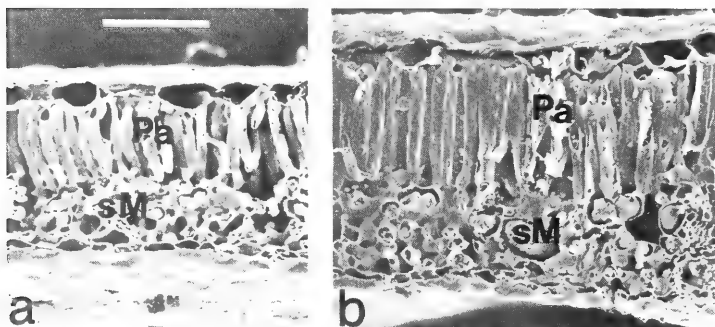


FIG. 5.

Leaf sections of *O. cupheoides* of individuals from a habitat (a) exposed to, and (b) protected from fire (population Pypkop, Puff 790211–4/1). Note the difference in thickness and the much more closely spaced, large palisade cells (Pa) and denser spongy mesophyll (sM) in b. The upper epidermis is covered by a massive, \pm wrinkled cuticle and the outer walls of the epidermis cells are much thickened in b, whereas the cuticle is thin and hardly detectable and the outer walls are not conspicuously thickened in a (this, however, is not clearly visible in the micrographs). The bar represents 0,1 mm; the magnification of a and b is the same.

Other factors, such as substrate or moisture differences (plants growing in rock crevices vs. plants in shallow depressions on top of rock slabs, for example), did not seem to contribute substantially to the variability.

Observations similar to the ones described above were made in the other localities visited: *O. cupheoides* is a species always associated with these rocky

TABLE 2.

Morphological differences between individuals from habitats protected from and exposed to fire of a population of *O. cupheoides* (summit of Pypkop, Woodbush Forest Reserve, Eastern Transvaal; Puff 790211-4/1) In brackets: numbers of individuals investigated.

	protected from fire (27)	exposed to fire (13)
habit	mats or cushions, c. 100–150 mm tall; stems woody, \pm prostrate, much-branched. Figs 3 and 4b	\pm erect stems arising from woody base, c. 190–300 mm tall; usually unbranched. Fig. 4a
stems diam. at base	c. (3) 5–7 mm	c. 1–1.5 mm
longest internodes	(2) 4–8 (10) mm	(25) 30–40 mm
hairs length	in 2 rows or all over, only near tips of branches; 0.3–0.4 mm	all over, whole length of stems; 0.6–0.8 mm
short shoots produced in axils of midstem leaves	none	present nearly at each node
leaves size	11–15 \times 4.5–5 mm	15–21 \times 8–10 mm
shape	lanceolate	ovate-lanceolate
hairs	none or very few on midrib above	midrib above and below, margin (few); sometimes also on upper surface
texture	(sub)coriaceous; also see Fig. 5b	\pm membranaceous; also see Fig. 5a
inflorescences	15–30 (45) mm (fruiting)	(30) 60–80 mm (fruiting)
pedicels, length	0.5–0.7 mm	0.8–1 mm
enlarged, foliaceous calyx lobes	3.5–5 \times 1.2–1.5 (2) mm	4.5–5.5 \times 1.5–2.2 mm

areas. The majority of individuals in a population were almost always found in "fire-proof" situations, whereas relatively few were in habitats that are in reach of at least exceptionally strong fires. Plants exposed to fires were always similar to the forms described above (Fig. 4a), although the differences between cushion- and mat-forming plants and fire-exposed plants were not always as "extreme" as in the Pypkop example.

In contrast to *O. cupheoides*, *O. inyangana* subsp. *inyangana* is primarily a plant of regularly (or at least occasionally) burnt grasslands. Sometimes, however, plants are also found in habitats not reached by fires such as "grassy islands" surrounded by large areas of solid rock. An example is the population of *O. inyangana* on the summit of Castle Beacon, Vumba Mts. (Puff 790128-1/4); once again, the morphological differences between individuals exposed to and protected from fires are striking (Table 3; Fig. 6). The differences observed were largely the same as in *O. cupheoides*, although (with subsp. *inyangana* being primarily a plant of burnt grasslands) woody-stemmed forms were the exception rather than the rule.

TABLE 3

Morphological differences between individuals from habitats protected from and exposed to fire of a population of *O. inyangana* subsp. *inyangana* (summit of Castle Beacon, Vumba Mts.; Puff 790128-1/4). In brackets: numbers of individuals investigated.

	protected from fire (5)	exposed to fire (10)
habit	± erect, woody stems, to c. 750 mm long; much-branched. Fig. 6a	erect, non-woody stems, to c. 300-400 mm long; usually unbranched. Fig. 6b
stems diam. at base	c. (2) 3-5 mm	c. 1-2 (2,5) mm
longest internodes	(4) 6-10 mm	(18) 20-30 (32) mm
hairs	hairy all over, only near tips of branches;	hairy all over, upper two thirds of stems;
length	0,4-0,6 mm	0,5-0,8 mm
short shoots produced in axils of midstem leaves	none or very few	present at each node
leaf arrangement	always decussate	in whorls of 3 on most stems
leaves size	7-11 × 3,8-4,5 mm	12-16 (19) × 7-9 mm
shape	ovate-lanceolate	± ovate
hairs	none or few on midrib below	midrib below and usually also on upper surface
texture	—	—
inflorescences	ca. 10-15 mm; few-flowered	ca. 20-25 mm; many-flowered
enlarged, foliaceous calyx lobes	3-5 × 1,5-2 mm	4-6 × 1,5-2,5 mm

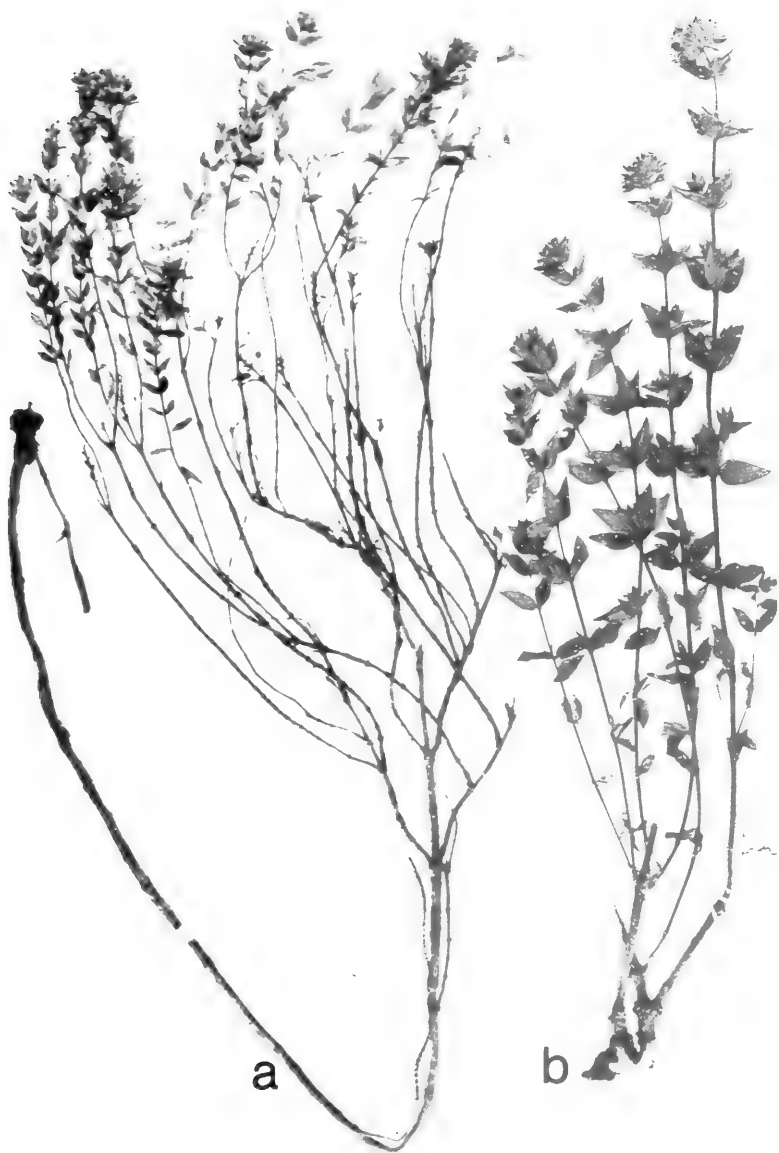


FIG. 6.

Individuals of *O. inyangana* subsp. *inyangana* from a habitat (a) protected from, and (b) exposed to fire (population Castle Beacon, Puff 790128-1/4). a and b: $\times \frac{1}{2}$. Explanations in the text.

Because of the peculiar topography of the locality, the number of morphological intermediates was markedly less (10 % or less of the individuals) than in the Pypkop population of *O. cupheoides*.

According to my field observations, *O. calycophylla* subsp. *calycophylla* nearly always occurred in habitats clearly out of reach of fire. Individuals that had been exposed to fire were never observed by me in the field, but some collections (*Esterhuysen* 21445 or *Strey & Schlieben* 8529 from the Blouberg, or *Gillett* 4729 from the Soutpansberg) almost certainly represent fire exposed forms.

O. calycophylla subsp. *verdcourtii* was always found in open, sometimes rocky grassland subjected to fires. Correspondingly, the plants were similar in habit to *O. inyangana* subsp. *inyangana*: after burning, numerous \pm erect flowering stems arise from often massive woody bases. The (\pm moderate) variability displayed by the subspecies, therefore, is either purely genetic or may be attributed (to a certain extent) to other unknown environmental influences.

The Influence of Environmental Factors Other Than Fire *Light*

All taxa studied in the field were found to occur in full sunlight with the exception of some Magaliesberg populations of *O. calycophylla* subsp. *calycophylla*. These were encountered on perpendicular rock faces of wooded kloofs: individuals growing near the top of the rock faces were fully exposed to the sun, while individuals growing near the bottom of the gorges were in the shade of tall trees for most of the day. Individuals of a population growing in shade could often be distinguished from those growing in sun by their thinnish stems with widely spaced, large and membranaceous leaves and very few-flowered inflorescences.

The inconsistent occurrence of such large-leaved forms in shady habitats may indicate that light is not the only factor involved. It is possible that soil moisture (degree of dampness of shade habitats) has a certain influence but this was not checked.

Altitude

The population of *O. inyangana* subsp. *inyangana* occurring from the eastern base of Mt. Inyangani to the summit plateau (*Puff* 790125-1/2a-f) was studied in detail. Samples were collected at six different stations between 2 150 and 2 580 m altitude; all collections originated from recently burnt grassy areas.

An analysis of these gatherings showed that there is a \pm continuous decrease in plant height with increasing altitude. The tallest plants occur in the lowest altitudes, small, mat- or cushion-forming individuals are confined to the highest altitudes (compare Figs 7a and b). In the latter, shorter internodes in the vegetative region are associated with shorter, fewer-flowered inflorescences. The



FIG. 7.

Two individuals from the population of *O. inyangana* subsp. *inyangana* stretching from the E base of Mt. Inyangani to the summit plateau (Puff 790125-1/2). a: from the E base (2 150 m), b: from the summit (2 580 m). a and b: $\times \frac{1}{2}$. Explanations in the text.

leaves of cushion- or mat-forms are relatively shorter and wider; they are always arranged decussately, whereas individuals from lower altitudes have, at least on the main-stems, the leaves arranged in whorls of three.

TAXONOMY

Otiophora Zucc.¹

Dwarf shrubs, under-shrubs or perennial herbs with massive, woody bases. *Stems* much- to few- or unbranched, \pm terete to obscurely 4-angled; at least younger parts covered with yellowish to whitish, \pm spreading or curled multicellular hairs, older parts often becoming glabrous, dark brown to dark grey, with the epidermis flaking off. Stems and lateral branches often with \pm inconspicuous short shoots. *Leaves* decussate, in true whorls of 3(4) or pseudoverticillate (owing to presence of well-developed short shoot leaves); *petioles* very short or obsolete; blades variable in size and shape, \pm ovate to linear-lanceolate, \pm acute to obtuse at the apex, membranaceous to coriaceous, with 2-4 usually \pm indistinct lateral veins on either side of the midvein, glabrous or hairy on margins, veins or surfaces, margins \pm flat to slightly revolute; *stipules* divided into 3-5(-7) gland-tipped \pm linear segments (setae), the median seta usually (much) longer than the others. *Inflorescences* head- or spike-like, usually elongated when in fruit. *Buds* with a limb abruptly expanded into a \pm pyriform, ovoid or subcylindrical head, distinct from the tube, or claviform, limb and tube not distinct from each other. *Flowers* (strongly) protandrous, on short, persistent pedicels; *calyx lobes* 5, one enlarged, foliaceous (sometimes flanked by a second, slightly enlarged lobe), other lobes minute, setiform; *corolla* 5-merous, glabrous or throat of corolla and corolla tube hairy inside, tube distinctly filiform or narrowly infundibuliform, lobes (\pm) lanceolate to oblong, (\pm) acute at the apex; *stamens* 5, exserted, *filaments* inserted at/near the throat, filiform, \pm erect and stiff, glabrous or hairy near the base, anthers oblong, yellowish to whitish; *style* glabrous, filiform, stigma bifid, lobes filiform; *ovary* bilocular (but one carpel sometimes smaller and \pm reduced), sparsely to densely covered with short, whitish hairs. *Fruits* splitting into two mericarps; mericarps dorsally convex, ventrally plane or slightly concave. *Seeds* \pm oblong to \pm ovoid, granulated, dorsally convex, sometimes keeled, ventrally flat or (slightly) concave.

KEY TO THE SPECIES AND SUBSPECIES

- | | |
|---|---|
| 1. Corolla tubes distinctly filiform, c. 0.1-0.2 mm wide; buds with a limb (abruptly) expanded into a \pm pyriform, ovoid or subcylindrical head | 2 |
| Corolla tubes narrowly infundibuliform, c. (0.2)0.3-0.5 mm wide at the base and c. (0.6)0.7-1.5(1.8) mm at the throat; buds claviform, limb and tube not distinct from each other | 4 |

¹ Description valid only for southern African taxa.

2. Flowering and fruiting inflorescences lax, spike-like, c. (15)40–150(250) mm long; from tropical Africa extending into Zimbabwe (Rhodesia), also on Madagascar **O. scabra** Zucc. subsp. **scabra** (see footnote, p. 298)
Flowering inflorescences, condensed, head-like, c. 10–25 mm long, fruiting inflorescences often elongated, up to 70 mm long; only in the Transvaal and Natal ... 3
3. Leaves small, (5)7–13(16) × (2)2,5–5(6) mm; foliaceous calyx lobes c. (2,2)2,5–4 mm long; irregularly branched dwarf shrubs with ± much-branched, woody stems; ± widely distributed in the Transvaal and Natal 1A. **O. calycophylla** subsp. **calycophylla**
Leaves larger, (14)16–28 × 5–10 mm; foliaceous calyx lobes c. 3,8–5,5 mm long; perennial herbs or under-shrubs with massive, woody bases and few- or unbranched, ± herbaceous stems; endemic to the eastern Soutpansberg 1B. **O. calycophylla** subsp. **verdcourtii**
4. Throat of corolla glabrous 2. **O. cupheoides**
Throat of corolla distinctly hairy 5
5. Leaves ovate or ovate-lanceolate, (7)10–33 × (3,8)4,5–13 mm, decussate or in whorls of 3(–4) 3A. **O. inyangana** subsp. **inyangana**
Leaves linear-lanceolate or lanceolate, 10–40(47) × 1,6–6(7,5) mm, strictly decussate 6
6. Leaves 10–18 × 1,6–3,5(4) mm; corolla tube (4) 5,5–9 mm long 3B. **O. inyangana** subsp. **parvifolia**
Leaves 23–40(47) × 3–6(7,5) mm; corolla tube (3,2)3,8–4,5(5) mm long 4. **O. lanceolata**

1. **O. calycophylla** (Sond.) Schlecht. & K. Schum. in Bot. Jahrb. **30**: 416 (1901).
Anthospermum calycophyllum Sond. in Fl. Cap. **3**: 31 (1865). Syntypes: Transvaal, Magaliesberg, *Burke & Zeyher* (K!, as *Burke 94*; E!, as *Zeyher 94*; K!, P!, S!, as *Zeyher 1376*), *Sanderson s.n.* (K!, as "Transvaal"), *Sutherland s.n.* (?).

Two subspecies are recognized:

1A. **O. calycophylla** subsp. **calycophylla** (Fig. 9a)

O. hebe Verdc. in J. Linn. Soc. Bot. **53**: 402 (1950). Type: Transvaal, Blauwberg, on rock above Nek and near top of Nek, *Pole Evans 900* (K!, holo.; PRE!).

Several- to many-stemmed, irregularly branched dwarf shrubs. *Stems* ± much-branched, sprawling, ascending to ± erect, (60)100–300(400) mm long, c. 1,5–6 mm in diam. at the base, c. 0,8–1,5 mm in the mid-stem region; hairs c. 0,1 mm, occasionally up to 0,6 mm long, sometimes in two vertical rows. Longest internodes (2)4–20(33) mm. *Leaves* decussate; *petioles* obsolete or c. 0,3–1(1,5) mm long; blades usually spreading, (5)7–13(16) × (2)2,5–5(6) mm, ± ovate to ovate-lanceolate or oblong-lanceolate, coriaceous to subcoriaceous, glabrous, with short forwardly directed hairs on margins and/or upper surface or hairy all over. *Stipular setae* 3–5, c. 0,5–1 mm long, sometimes hairy at the base. *Inflorescences* few- (20- or less-) flowered; condensed, head-like, c. 10 mm or less in diam. when in flower, slightly elongated, c. 10–30(50) mm long when in fruit. *Buds* with a limb (sometimes abruptly) expanded into a pyriform or ±

ovoid head; in near mature buds, tubes c. 1,5–3,5 mm long, heads c. (1)1,3–2,5 × 1–1,8 mm. *Flowers* white, pale pink, mauvish-pink to mauve; enlarged, foliaceous calyx lobe c. (2,2)2,5–4 × 0,9–1,5 mm, ± ovate to ovate-lanceolate, glabrous, with short bristles on margins or (rarely) hairy all over, setiform lobes c. 0,1–0,5 mm, usually glabrous; *corolla* glabrous, tube (2)2,5–5(5,8) mm long, filiform, c. 0,1–0,2 mm in diam. at the base, c. 0,2–0,4(0,5) mm at the throat, lobes (1,5)1,8–3,2(3,7) × 0,4–0,8(1) mm, ± lanceolate; *filaments* c. 1,2–2,5 mm long, glabrous, anthers c. 0,4–0,8(1) × 0,2–0,4 mm; *style* (2,7)3,5–7 mm, stigma lobes c. (0,5)0,8–1,5(2) mm, *ovary* c. 0,8–1,2 × 0,5–0,7 mm, sparsely to densely covered with hairs less than 0,1–0,3 mm long. *Fruits* greenish or brownish; each mericarp (1,5)1,7–2,2(2,4) × (0,7)0,8–1,2 mm. *Seeds* blackish, c. 1,1–1,5 × 0,4–0,5 mm, ± oblong, dorsally convex, ventrally slightly concave.

Chromosome Number: $n = 17$, $2n = 34$.

Average Pollen Diameters: 31,8–34,2 μm .

Habitat: Usually in rock crevices, often on perpendicular rock faces, rock krantzies, cliffs; commonly in shallow, quartzite derived soil mixed with humus; usually growing in full sun, rarely in shady (and ± damp) situations. Ca. 1 200–1 700 m.

Flowering Period: December to March (April); odd flowering specimens also seen from June, July and October.

Distribution (map, Fig. 10): Disjunct. Magaliesberg, Blouberg, and western and central Soutpansberg, Loskopdam; Natal Midlands and Zululand.

Comments: In 1973, Verdcourt raised doubts about the distinctiveness of *O. calycophylla* and *O. cupheoides*. After extensive field observations and critical screening of the herbarium material now available, there is no doubt, however, that the two are distinct entities, a view expressed by Verdcourt (1950) in his original monograph of the genus. While the two may occasionally resemble each other vegetatively to a certain extent (see chapter VARIABILITY), they clearly differ in floral structure: *O. calycophylla* always has a distinctly filiform, narrow corolla tube (Fig. 8a), *O. cupheoides* always an unmistakably narrowly infundibuliform tube, much wider at the throat than at the base. While the buds of *O. cupheoides* are claviform (limb and tube not distinct from each other; Fig. 8b), *O. calycophylla* buds always have filiform tubes clearly distinct from the ± pyriform, ovoid to ± subcylindrical heads (limbs).

In *O. calycophylla*, the bud shape varies slightly in that the tubes either merge gradually into the heads or are expanded abruptly into the heads. It seems that this, to a certain extent, depends on the age of the buds (often difficult to assess!).

Verdcourt's (1950) view that *O. hebe*, although closely allied to *O. calycophylla*, differs in having its "leaves arranged very differently" (p. 402) cannot be upheld. The two collections of *O. hebe* from Blouberg known to Verdcourt are portions of plants with very closely-spaced, quite coriaceous leaves crowded

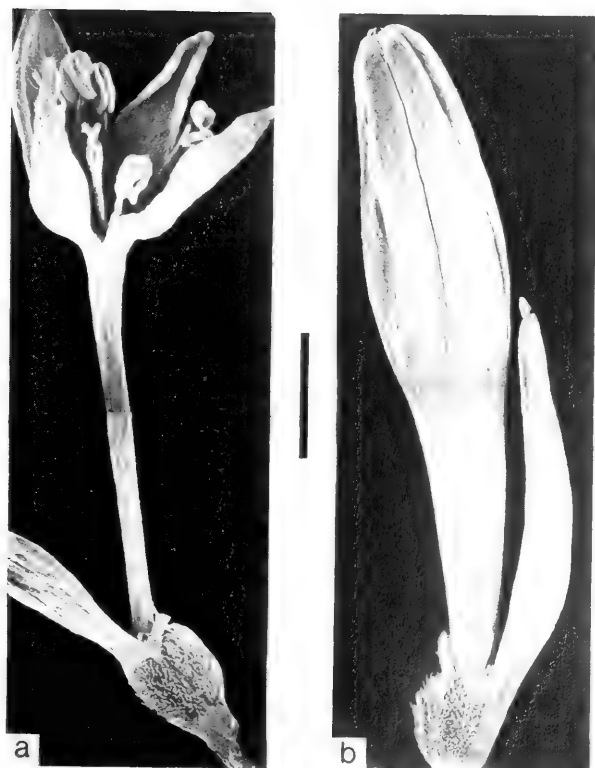


FIG. 8

a: Flower of *O. calycophylla* subsp. *calycophylla* (\pm filiform corolla tube); b: bud of *O. cupheoides* (narrowly infundibuliform corolla tube. The bud is fairly young and the tube has not yet reached its full length; its shape, however, will remain the same). The bar represents 1 mm. (a: Puff 790307-2/1, b: Puff 790211-4/1)

near the tips of the branches. These features are found in and are typical for old, woody plants of *O. calycophylla* subsp. *calycophylla* throughout its whole range of distribution. *O. hebe* and *O. calycophylla* (subsp. *calycophylla*) thus are inseparable vegetatively as well as with regard to floral and fruit characters.

Some unusually large-leaved forms of subsp. *calycophylla* from the Magaliesberg (Marais 297, Repton 708, for example; see chapter VARIABILITY) with shoots with long internodes resemble subsp. *verdcourtii* vegetatively, but are characterized by the small flowers typical for all other Magaliesberg collections. Some collections from the Blouberg and central Soutpansberg are difficult to assign to a subspecies; they may be plants belonging to subsp. *calycophylla* that have been exposed to fire (see VARIABILITY).

The distribution of subsp. *calycophylla*, in contrast to that of subsp. *verdcourtii* and *O. cupheoides*, is a rather disjunct one (see map, Fig. 10). It is of interest to note that there seems to be some correlation between geographic distribution and flower size and colour: Magaliesberg specimens tend to have small, white flowers (although the buds are often tinged pink), specimens from the Blouberg and the western and central Soutpansberg tend to have slightly larger, pink or mauve flowers, and Natal collections have small, pink flowers.

COLLECTIONS

TRANSVAAL—2229 (Waterpoort): road leading off to the W at the Mountain Inn, c. 32 km, Dr. Bird's farm (-DC), Meeuse 9780 (NH, PRE, S); —, c. 13.5 km, between Farms "Alaska" and "Bluegumspoort", c. 1 550–1 600 m (-DD), Puff 791202–3/2 (J); pass N of Louis Trichardt, between Louis Trichardt and Wylies Poort, Gillett 2877 (BOL, NBG).

—2328 (Baltimore): Blouberg, c. 1 700 m (-BB or 2329 -AA), Esterhuysen 21445 (BOL, PRE), Smuts & Pole Evans 869 (PRE, STE; K- as "Pole Evans 869"), Pole Evans 900 (K, PRE; type of *O. hebe*), Scholes sub Puff 781218–1/1 (WU), Strey & Schlieben 8497 (PRE), 8529 (B, PRE, SRGH), van Niekerk 21445 (PRE); —, Mohlakeng Plateau, Codd & Dyer 8982 (PRE).

—2329 (Pietersburg): Soutpansberg, (above) Louis Trichardt (-BB), Breyer 2277 (PRE), Hutchinson 2018 (BOL, K, PRE, SRGH), Koker 9 (PRE); —, Farm "Peover" near Louis Trichardt, Verdoorn 2235 (PRE).

—2527 (Rustenburg): Magaliesberg, Castle Gorge, Farm "Elandskraal 469 JQ" (-AD), van Wyk 116 (PRE); —, Farm "Rainhill" near Rustenburg, c. 1 220 m (-CA), Codd 1078 (PRE); —, Rustenburg Kloof, Collins 7039 (PRE), Prosser 1839 (PRE); —, Rustenburg Nature Reserve, Jacobsen 711 (PRE), 817 (PRE); —, Rustenburg, Tierkloof, Venter 249, 416, 670, 679 (all PRE); —, "Crystal Waters", de Winter 8301 (PRE), Repton 5855 (PRE); —, Bestieg's Kloof, 1 700 m (-CB), Mogg 34474 (J, SRGH); —, above "Berghheim" near Kroondal, Young 27490 (PRE); —, Farm "Kloofwaters", c. 1 500 m (-CD), Puff 790307–2/1 (BR, J, WU), 790706–1/1 (WU); —, Brits Distr., kloof opposite Wolhuterskop turnoff

on Rustenburg road (-DA), *Marais* 287 (PRE); —, —, "Jacksonstuijn", *Mogg* 14233 (PRE), *van Vuuren* 172 (PRE); —, Hartebeespoort dam, near "Jacksonstuijn" (-DA/-DB), *Repton* 708 (PRE); —, Hartebeespoort dam (-DB), *Pienaar* 863 (PRE). Imprecise localities (2527-C or -D): Rustenburg Distr., Magaliesberg, *Burke* 94 (K; type of *O. calycophylla*), *Esterhuysen* 15569 (BOL), *Nation* 64 (BOL, K), 216 (K, MO), *Zeyher* 94 (E; type of *O. calycophylla*), 1376 (K, P, S; type of *O. calycophylla*).

—2528 (Pretoria): Wonderboom Poort (-CA), *Mogg & Dyer s.n.* sub PRE 41846 (PRE).

—2529 (Witbank): Loskopdam Nature Reserve (-AD), *Mogg* 29534 (J; \pm atypical); —, NE of Tweeloopfontein, *Theron* 1292 (PRE; \pm atypical).

Imprecise localities: Zoutpansberg, *Compton* 18074 (NBG), *Gillett* 4729 (PRE x2), 4730 (PRE x2); "Transvaal", *Sanderson s.n.* (K).

NATAL—2831 (Nkandla): Nkandla, c. 1 220–1 520 m (-CA), *Wylie* sub *Wood* 8866 (BOL, NH).

—2930 (Pietermaritzburg): Ahrens, Farm "Mowbray", c. 1 520 m (-BB), *Fisher* 975 (NH, NU).

1B. *O. calycophylla* subsp. *verdcourtii* Puff. subsp. nov.; habitu saepe erecta, caulibus non ramosis vel ramis lateralibus paucis et internodiis longioribus, foliis (14)16–28 \times 5–10 mm, saepius ellipticis-lanceolatis vel plus minusve lanceolatis, calycis lobis foliaceis c. 3,8–5,5 \times 1–1,8 mm, et corollae tubo saepius longiore, usque ad 6,5 mm longo, a subsp. *calycophylla* differt. (Fig. 9b)

Type: Transvaal (Venda), Sibasa Distr., Tate Vondo Forest Reserve, 1 160, *Hemm* 352 (PRE, holo.; J).

[*O. calycophylla* sensu Hutch., *Botanist S. Afr.* 671 (1946), quoad pl. cit. solum (*Hutchinson* 4150a). "14. *Otiophora* sp.". Verdc. in *J. Linn. Soc. Bot.* 53: 411 (1950). (*Hutchinson & Gillett* 4367, K!).]

Usually many-stemmed, erect to \pm sprawling perennial herbs or undershrubs with a massive, woody base up to c. 20 mm in diam. *Stems* few- or sometimes unbranched, 260–400 mm, c. 0,8–3,5 mm in diam. at the base, c. 0,8–1 mm in the mid-stem region; hairs c. 0,2–0,4 (0,6) mm long, in two vertical rows or stems hairy all over. Longest internodes 15–45 mm. *Leaves* decussate; *petioles* c. 0,5–1,5 mm long; blades spreading to ascending, (14) 16–28 \times 5–10 mm, ovate-lanceolate and broadest near the base, elliptic-lanceolate and broadest near the middle, or \pm lanceolate, subcoriaceous, glabrous or hairy on midvein above and/or below, or with scattered hairs on upper surface. *Stipular setae* 3–5, c. 0,7–1,7 mm long. *Inflorescences* c. 20- to 30-flowered; head-like, c. 10–25 mm in diam. when in flower, elongated, rather spike-like, c. 20–70 mm long when in fruit. *Buds* with a limb \pm abruptly expanded into a \pm ovoid to subcylindrical head; in near mature buds, tubes c. 1,5–2 mm long, heads c. 2–2,5 \times 1–1,5

mm. Flowers pink, (pale) lilac or mauve; enlarged, foliaceous calyx lobe c. 3,8–5,5 × 1–1,8 mm, ± lanceolate to ± ovate-lanceolate, glabrous or sometimes a little hairy on the margins, setiform lobes c. 0,2–0,7 mm long, glabrous; corolla glabrous, tube 3,8–6,5 mm long, filiform, c. 0,2 mm in diam. at the base, c. 0,3–0,4 (0,5) mm at the throat, lobes 2,5–4 × 0,5–0,9 mm ± lanceolate; filaments c. 1,5–3 mm long, glabrous, anthers c. 0,5–1,1 × 0,3–0,5 mm; style 7–8,5 mm, stigma lobes c. 1–2 mm, ovary c. 0,8–1 × 0,5–0,7 mm, ± glabrous to densely covered with hairs c. 0,1–0,2 mm long, the carpel crowned by the enlarged calyx lobe sometimes less hairy than the other. Fruits greenish, greenish-brown to dark brown; each mericarp c. 1,7–2,2 × 0,8–1,2 mm. Seeds blackish, c. 1,2–1,6 × 0,4–0,6 mm, ± oblong, dorsally convex, ventrally slightly concave.

Chromosome Number: $n = 17$, $2n = 34$.

Average Pollen Diameters: 32,4–33,6 μm .

Habitat: In (rocky) grassland; often in sandy loam; usually growing in full sun. Ca. 750–1 500 m.

Flowering Period: October to February; odd flowering specimens seen from July and August.

Distribution (map, Fig. 10): Endemic to the eastern Soutpansberg (high rainfall areas).

Comments: As far as habitat and distribution are concerned, subsp. *verdcourtii* is well demarcated from subsp. *calycophylla*: The subspecies occurs primarily in grassland and is (presumably¹) endemic to the eastern and much wetter part of the Soutpansberg range. Floral characters (filiform corolla tubes) accentuate the close relationship to subsp. *calycophylla*; subsp. *verdcourtii*, in general, has slightly longer corolla tubes and larger lobes, but there is some overlap with the other subspecies. Vegetatively, typical forms of the two subspecies are easily distinguished by differences in habit (compare Figs 9a and b), internode lengths and leaf size and shape, but again, this is not always so. I, therefore, have hesitated to raise *verdcourtii* to species rank.

COLLECTIONS

TRANSVAAL—2230 (Messina): Entabeni (-CC), *Hutchinson 4150a* (?K), *Taylor 715* (PRE); Piesanghoek, c. 1 220 m, *Gerstner 5737* (PRE); Sibasa (Distr.), Mt. N. of Pepiti (=Phiphidi), c. 900–1 500 m (-CD), *Hutchinson & Gillette 4367* (K), *Smuts & Gillett 3249* (PRE, STE), *3270* (PRE), *3270** (PRE, STE); —, Tate Vondo For. Res., Tate Vondo, 1 100 m, *Hemm 352* (J, PRE);

¹ Collections of subsp. *verdcourtii* with precise information on collecting localities all originate from the eastern part of the Soutpansberg range; if others, only stating "Soutpansberg" as locality, in fact do come from the eastern part, is impossible to determine. On my own collecting trips, I have found subsp. *verdcourtii* only in the wet eastern part, and subsp. *calycophylla* only in the much drier, western part of the Soutpansberg.



FIG. 9.
Individuals of *O. calycophylla* subsp. *calycophylla* (a) and subsp. *verdcourtii* (b) in their natural habitat. a: a large-flowered form from the western Soutpansberg (Puff 791202-3/2), b: a plant from the grassland near Vondo Lookout (= \pm type locality; Puff 791201-1/1). The bar represents 50 mm in a and 100 mm in b.

type of ssp. *verdcourtii*); —, Vondo Plantation, near Vondo Lookout, c. 1 150 m, *Puff* 791201-1/1 (J); —, —, edge of Tate Forest ("Holy Forest"), c. 1 300 m, *Puff* 791201-3/1 (J); —, —, Tshamanyatsha Plantation, c. 1 000-1 200 m, *Puff* 791201-4/2 (J), -5/1 (J); —, summit of Khongoroni Mt., c. 1 450 m, *Puff* 791202-2/2 (J); Muchimdudi Falls, c. 1 220 m, *Bruce & Kies* 10 (PRE); (Lake) Funduzi, *Bremekamp & Schweickerdt* 364 (PRE); Makonde (Mission Station), c. 760 m (-DC), *van Warmelo* 5116/7 (PRE); —, top of Makonde Hill, c. 900 m, *Codd* 6864 (PRE, SRGH).

—2329 (Pietersburg): Louis Trichardt (Distr.), Hangklip, c. 1 700 m, *Gerstner* 5993 (PRE), *Bremekamp & Schweickerdt* 430 (PRE ×2); —, Bonzberg, *Moss* 14588 (J ×2).

—2330 (Tzaneen): 15 km E of Louis Trichardt (-AA), *Schlieben* 7331 (BR, J); Tshakoma (-AB), *Obermeyer* 30107 (PRE).

Imprecise locality: Zoutpansberg, *Gillet* 4737 (PRE ×2).

Localities not traced: Louis Trichardt Distr., Farm "Rustfontein", Zoutpansberg plateau, *Schlieben & Strey* 8355 (B, G, PRE, SRGH, W); Luvimbi, *Junod* 21121 (PRE).

2. *O. cupheoides* N.E.Br. in Hook. Icon. Plant **15**: t. 1454, 1884). Type: Transvaal, Houtbosch, *Rehmann* 5901 (K!, holo.; BOL!).

O. hirsuta Bär in Vierteljahresschr. naturforsch. Ges. Zürich **68**: 435 (1923). Type: Transvaal, Shilouvane, rocks at Marovoung and Mamotsuiri, *Junod* 856 (Z!, holo.; K).

O. cupheoides var. *hirsuta* (Bär) Verdc. in J. Linn. Soc. Bot. **53**: 40 (1950).

O. densiflora Bär in Vierteljahresschr. naturforsch. Ges. Zürich **68**: 436 (1923). Type: Transvaal, Shilouvane, *Junod* 856a (Z!, holo.).

O. cupheoides var. *macrostemon* Verdc. in J. Linn. Soc. Bot. **53**: 400 (1950). Type: Transvaal, Saddleback Range, Barberton, 5 000 ft., Galpin 729 (K!, holo.; BOL!, PRE ×2!, SAM!).

Several- to many-stemmed, sprawling, mat- or cushion-forming dwarf shrubs; sometimes perennial herbs with massive woody bases up to 20 mm in diam. *Stems* much-branched (few- or unbranched in fire-exposed individuals), 80-450 (600) mm long, c. (1) 1,5-5,5 (7) mm in diam. at the base, c. 0,8-1,5 mm in the mid-stem region; hairs c. 0,3-0,8 mm long, in two vertical rows or stems hairy all over. Longest internodes c. (2) 4-25 mm (typical forms), or c. (20) 30-40 (45) mm (fire-exposed individuals). *Leaves* decussate; petioles obsolete or 0,5-1,5 (2) mm long; blades ± spreading, (9) 11-22 (36) × (3,5) 4-8 (13) mm, ovate-lanceolate and broadest near the base or ± lanceolate, glabrous or hairy on margins, midvein above and/or below, lateral veins, upper surface, or with a dense cover all over. *Stipular setae* 3-5 (-7), the longest c. 0,7-1,8 mm, glabrous or sometimes a little hairy. *Inflorescences* few- to many-flowered;

head-like, c. 10–20 mm in diam. when in flower, sometimes much elongated, spike-like, up to 45 (60) mm (typical forms) or to c. 120 (170) mm (fire-exposed individuals) long when in fruit. *Buds* claviform. *Flowers* white (sometimes tinged pink, reddish or faint purple when in bud); enlarged, foliaceous calyx lobe c. (3,5) 4–8 (10) \times (1) 1,2–2 (2,2) mm, \pm lanceolate, glabrous or a little hairy, setiform lobes (0,2) 0,4–0,8 (1,2) mm long, usually glabrous; *corolla* glabrous, tube 4–12 mm long, narrowly infundibuliform, (0,2) 0,3–0,4 (0,5) mm in diam. at the base, (0,6) 0,8–1,5 (1,8) mm at the throat, lobes (2,5) 3–4,6 (5,5) \times 0,6–1,2 mm, lanceolate or oblong-lanceolate; *filaments* c. (2,5) 2,8–3,5 (4,2) mm long, glabrous, anthers c. 0,6–0,9 \times 0,2–0,4 mm; *style* 7–12 (15) mm, stigma lobes c. (0,7) 1–1,5 (2) mm, *ovary* c. 0,7–1,2 \times 0,5–0,8 mm, sparsely to densely covered with hairs c. 0,2–0,5 mm long, the carpel crowned by the enlarged calyx lobe sometimes less hairy than the other, smaller, \pm reduced. *Fruits* greenish, brownish or blackish; each mericarp 1,8–2,5 \times 0,8–1,2 mm, the mericarp crowned by the enlarged calyx lobe sometimes smaller, without seed. *Seeds* black or brownish-black, c. 1,2–1,4 \times 0,5–0,7 mm, \pm ovoid to oblong, dorsally convex, ventrally plane to strongly concave.

Chromosome Number: $n = 17$, $2n = 34$.

Average Pollen Diameters: 32–33,4 μm .

Habitat: Usually in cracks of rocks or depressions of flat rocks; in rocky outcrops, or in rocky grassland in rock clumps or between rocks; usually in shallow (black reef) quartzite or granite (and sandstone?) derived soil mixed with humus; normally growing in full sun. Ca. 1 100–2 150 m.

Flowering Period: November to April; odd flowering specimens also seen from June, July and September.

Distribution (map, Fig. 10): Along the Drakensberg escarpment from the eastern Transvaal to Swaziland.

Comments: Neither var. *macrosiphon* nor var. *hirsuta* should be retained.

Within the species, there is a continuous range of corolla tube lengths from 4 to 12 mm, making it highly artificial to separate plants with longer corolla tubes as var. *macrosiphon*. Corolla tube lengths were, furthermore, also found to vary considerably within individual plants and within populations.

Hairiness of the stems ranges from two lines of hairs to a denser cover, hair lengths from c. 0,3–0,8 mm. Leaves are either glabrous or have hairs along the veins, along the veins and scattered on the surfaces, or are densely hairy all over. Again, hairiness can vary within a population (see Table 2). The population of *O. cupheoides* in the Mamotswiri Peak area (Puff 791208–1/1; type locality of *O. hirsuta*) consists of plants that are indeed hairier than all others within the species, but it does not seem justified to separate this population as var. *hirsuta*, if the variability of the indumentum within the species as a whole is taken into account.

The range of distribution of *O. cupheoides*, following the Drakensberg

escarpment from the eastern Transvaal to Swaziland, is a very closed and well-defined one. The only collection, seemingly "out of place", *Rogers 19055* from "Waterberg Div., Leeupoort, Sept. 1917" may well have come from The Downs. The collection is inseparable from *Rogers 20185* and *22076*, both from The Downs. A comparison of collection numbers, collecting localities and dates makes a mixup of labels seem likely: *Rogers 19055*, supposedly from Leeupoort, was collected in September 1917, whereas *Rogers 20185*, the higher collection number, is dated July 1917; *Rogers 22076* was collected in December 1917.

Floral characters (claviform buds, narrowly infundibuliform corolla tubes) suggest a closer affinity of *O. cupheoides* to the species endemic to the Eastern Highlands of Zimbabwe (Rhodesia) and neighbouring Moçambique than to the South African *O. calycophylla*. *O. cupheoides*, *O. inyangana* and *O. lanceolata* are the only species in the genus with claviform buds and narrowly infundibuliform corolla tubes. Within this group, *O. cupheoides* is distinguished by having glabrous corollas.

COLLECTIONS

TRANSVAAL—2329 (Pietersburg): Iron Crown Mine, S of Haenertsburg, c. 1 850 m (-DD), *Mogg 16642* (PRE, SRGH); near summit of Iron Crown Mt., *Meeuse 9835* (PRE, S, SRGH); Houtbosch, *Rehmann 5901* (BOL, K; type of *O. cupheoides*); —, Kooimans Gat hill, c. 1 850 m, *Mogg 17200* (PRE); Houtboschberg, c. 2 150 m, *Schlechter 4456* (BOL, BR, GRA, PRE as "2317" = Tvl. Museum No.).

—2330 (Tzaneen): near Duiwelskloof, Grootbos Govt. For. Res., W of Westfalia Estate boundary, c. 1 620 m (-CA), *Scheepers 846* (BR, MO, PRE, SRGH, W); Woodbush For. Res., summit of Pypkop, c. 1 820 m (-CC), *Prosser 1920* (PRE), *Puff 790211-4/1A, -4/1B* (J, WU); Wolkberg near Haenertsburg (-CC or 2429-BB or 2430-AA), *Müller & Scheepers 189* (PRE), *Swart s.n.* (J).

—2430 (Pilgrim's Rest): The Downs, c. 1 350 m (-AA), *Junod 4265* (PRE × 3; 2 sheets as "19971" = Tvl. Museum No.), *Nel 100* (STE), *Rogers 20185* (GRA, PRE), *22076* (BOL, J, PRE, SAM, STE); The Downs area, *Puff 790210-4/2* (WU); —, Mamotswiri Peak above Farm "Hoffenden Heights", c. 1 700–1 800 m, *Puff 791208-1/1* (K, WU); Shilouvane, rocks at Marouvougne and Mamotsuiri, *Junod 856* (K, Z; type of *O. hirsuta*), *856a* (Z; type of *O. densiflora*); mts. near Trichardsdal, The Downs, 1 800 m (-AC?), *Vahrmeijer 2364* (MO, PRE, SRGH); Marieskop, c. 1 500–2 400 m (-DB), *Bos 1031* (B, LISC, PRE, STE), *Meeuse 9982* (PRE), *Merxmüller 593* (LISC, M, PRE), *Killick & Strey 2384* (G, PRE, SRGH), *van Dam 26305* (PRE), *van der Schijff 4523* (PRE, W), *4783* (PRE), *4831* (PRE, W), *6318* (PRE), *Werdermann & Oberdieck 1860* (B, BR, PRE), *1891* (B, PRE); above Pilgrim's Rest (-DD), *Taylor 509* (PRE); Graskop, *Holland s.n.* sub PRE *41844* (PRE), *Nel 125* (STE), *Rogers 20376* (PRE); —, "Edge of Berg", c. 1 600 m, *Galpin s.n.* sub BOL *24793*

(BOL), 14374 (PRE); Graskop Peak, c. 1 850 m, *Galpin* 14385 (PRE); "Fairy-land" (Private Nature Reserve) just outside Graskop, *van Jaarsveld* 1028 (MO, NBG, PRE), *Puff* 790704-1/1 (BR, J, WU); edge of escarpment, c. 1 km E of Graskop, 1 500 m, *Coetzee* 1439 (PRE); c. 17,6 km N of Graskop, c. 1 520 m, *Codd & de Winter* 3348 (PRE); between Pilgrim's Rest and Sabie, c. 1 070 m (-DD/ 2530 -BB), *Rogers* 23687 (BM, J, NH, PRE).

—2530 (Lydenburg): Tweefontein State Reserve near Sabie, 1 600–1 800 m (-BB), *Bernardi* 8976 (G).

—2531 (Komatipoort): Sabie Falls, S edge of gorge (-AA), *Burt Davy* 1553 (PRE); Barberton (-CC), *Thorncroft* 61 (K, NH), 2964 (PRE), 9608 (PRE); Saddleback Range near Barberton, c. 1 520–1 680 m, *Galpin* 729 (BOL, GRA, K, PRE × 2. SAM; type of *O. cupheoides* var. *macrosiphon*), *Puff* 780902-1/1 (BR, J, WU), *Thorncroft* 2183 (K); Ida Deyer Nature Reserve, 38 km SE of Barberton, 1 140 m, *Muller* 2051 (PRE); Barberton Distr., escarpment c. 41,5 km SE of Barberton, c. 1 220 m, *Lewis* 6333 (K, MO); —, near Havelock Mine, Transvaal side of border, c. 1 450 m, *Bayliss* 2745 (NBG).

Not traceable/doubtful localities: "Berg Plateau", *Mudd s.n.* sub BOL 24794 (BOL, K); Div. Waterberg, Leeupoort, *Rogers* 19055 (PRE).

SWAZILAND—2531 (Komatipoort): Piggs Peak Distr., Emlembe, c. 1 700 m (-CC), *Compton* 28496 (NBG, PRE); —, Emlembe Hill, Devils Bridge, *Hilliard & Burt* 3583 (E, NU); —, Havelock, c. 1 220 m, *Compton* 30636 (NBG, PRE, SRGH); —, Havelock road, c. 1 370 m, *Compton* 27678 (NBG); —, c. 5 km W of Piggs Peak, c. 1 250 m, *Compton* 7823 (PRE, SRGH); —, Peak Timber Plantations, A5 Section, Kobolodo Peak, c. 1 150 m, *Puff* 770118 -3/8 (WU).

—2631 (Mbabane): Mbabane Distr., Ngwenya Mt., c. 1 700–1 800 m (-AA), *Compton* 26529, 26682 (both NBG, PRE), *Puff* 790225-1/3 (WU); —, Bomvu Ridge, c. 1 700 m, *Compton* 32013 (NBG, PRE); Hlatikulu, c. 1 400 m (-CD), *Stewart* 54 (K, SAM).

Imprecise locality: "Swaziland", *Stewart* 9527 (PRE).

3. *O. inyangana* N.E. Br. in Kew Bull. 1906: 107 (1906). Type: Zimbabwe (Rhodesia), Manika Distr., Inyanga Mts., 6 000–7 000 ft., *Cecil* 203 (K!, holo.).

Two subspecies are recognized:

3A. *O. inyangana* subsp. *inyangana*

Usually many-stemmed, ± erect perennial herbs or under-shrubs with often branched, massive woody bases, c. 10–20 mm in diam., distinctly yellow in cross section; occasionally much-branched dwarf shrubs, sometimes forming cushions or mats. Stems generally few- or unbranched, 150–600 (750) mm long, c. (1) 1,5–4 (5) mm in diam. at the base, c. 0,8–1,5 (2) mm in the mid-stem region; hairs c. 0,4–0,8 mm long, in two vertical rows, or stems hairy all over. Longest

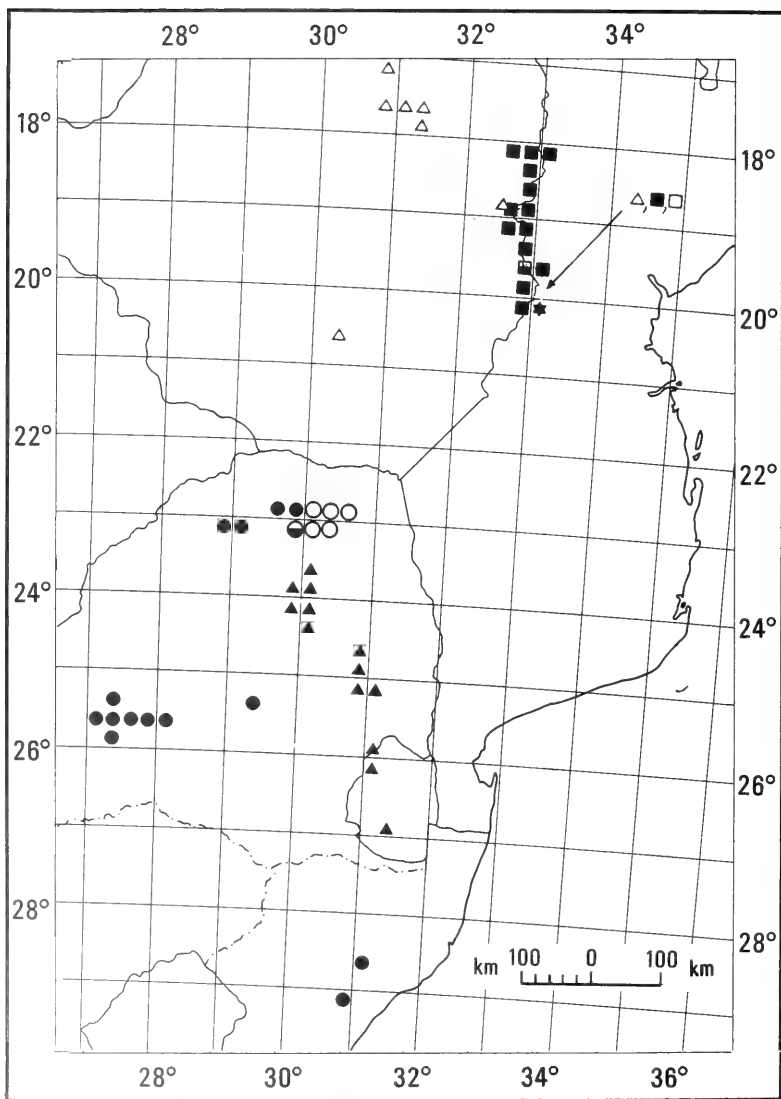


FIG. 10.

Distribution of *O. calycophylla* subsp. *calycophylla* (●) and subsp. *verdcourtii* (○; ●: both subspecies), *O. cupheoides* (▲), *O. inyangana* subsp. *inyangana* (■) and subsp. *parvifolia* (□; ■: both subspecies), *O. lanceolata* (★), and *O. scabra* subsp. *scabra* (△; southern Africa only).

internodes c. (15) 20–40 (60) mm (typical forms), or c. (4) 6–15 mm (dwarf shrubs, cushion-forming plants). *Leaves* decussate or in whorls of 3 (4), but sometimes apparently in whorls of 6 or more owing to presence of well-developed short shoot leaves; *petioles* c. 0.5–1.5 (2) mm or obsolete; blades erect, ascending or spreading, (7) 10–33 × (3.8) 4.9–13 mm, ovate to ovate-lanceolate, broadest at lower third or near the middle, glabrous or hairy on midvein, lateral veins and (occasionally) upper surface. *Stipular setae* 3 (–4–5), the longest c. 0.3–2 mm. *Inflorescences* usually many-flowered, often in groups of 2–3 (or more); head-like, c. (10) 20–40 mm in diam. when in flower, often much elongated, spike-like, c. 30–50 mm, occasionally up to 120 mm long when in fruit. *Buds* claviform. *Flowers* whitish, pale pink, pink, pale blue, mauve or purplish; enlarged, foliaceous calyx lobe c. (3.5) 4–8 × 0.8–2.2 (3) mm, ovate-lanceolate to lanceolate, often glabrous, setiform lobes c. 0.2–1 mm long; *corolla* usually glabrous outside, sometimes with a few hairs near the apex, throat of corolla and at least upper half of corolla tube ± densely hairy inside, tube (3.5) 4–6.5 (8) mm long, narrowly infundibuliform, c. 0.2–0.3 mm in diam. at the base, c. 0.5–1.2 mm at the throat, lobes (2.5) 3–5.5 × (0.4) 0.6–1.2 mm, lanceolate; *filaments* c. (2.5) 3.5–5.5 (6) mm long, usually hairy near the base, anthers c. 0.5–0.9 × 0.3–0.4 mm; *style* 6.8–11 mm, stigma lobes c. 0.6–1.1 (1.7) mm, ovary c. 0.7–1.2 × 0.5–0.8 mm, sparsely to densely covered with hairs 0.1–0.3 mm, sometimes up to 0.7 mm long, the carpel crowned by the enlarged calyx lobe often less hairy than the other. *Fruits* greenish to brownish; each mericarp 1.5–2.2 × 0.6–1.2 mm. *Seeds* black, c. (1) 1.2–1.4 × 0.5–0.8 mm, ± ovoid, dorsally convex or ± keeled, ventrally flat or concave.

Chromosome Number: $n = 17$, $2n = 34$.

Average Pollen Diameters: 26.6–29.4 μm .

Habitat: Usually in open grassland, sometimes at the edge of forest or scrub; rarely in rocky areas (amongst rocks) or disturbed sites (roadsides or plantations); commonly in clayey soils, (presumably) never on quartzite; usually growing in full sun. Ca. 1 200–2 580 m.

Flowering Period: (September) October to July.

Distribution (map, Fig. 10): Widely distributed and common in the Eastern Highlands of Zimbabwe (Rhodesia) from the Inyanga Distr. south to the Melsetter Distr., and extending across the border into Moçambique.

Comments: Subsp. *inyangana* is highly variable with regard to growth habit (stems erect, sprawling, or plants cushion- or mat-forming), indumentum, leaf shape and size and arrangement of the leaves in opposite pairs or in whorls of three or four, internode lengths, extensiveness of the inflorescence, length of the fruiting inflorescence, and shape and size of the foliaceous calyx lobe. Some of the environmental factors contributing to this plasticity are discussed under VARIABILITY.

Since several of the many "forms" of subsp. *inyangana* are frequently found

even in a single population, it seems unjustified to recognize any of them taxonomically (cf. Verdcourt, 1950: p. 398).

The arrangement of the leaves does not necessarily seem to be correlated with environmental factors. In typical grassland forms, for example, it was observed that stems arising from a common woody base may differ from each other by having their leaves arranged decussately or in whorls of three, or even four. Sometimes, leaf arrangement is not even constant on a single stem: leaves may be decussate below but in whorls of three above. Also the indumentum of leaves on stems arising from a common woody base may vary: on some stems, the leaves may be glabrous, in others slightly hairy.

COLLECTIONS

ZIMBABWE (RHODESIA)—1832 (Umtali): Inyanga (village?), c. 1 830 m (-BA), *Eyles 8510* (K, SRGH), *Hopkins 8652* (SRGH); Inyanga Distr., c. 13 km from Inyanga village along Troutbeck road, c. 2 050 m (-BB), *Rushworth 774* (BR, MO, SRGH); —, Troutbeck, *Rattray 1437* (SRGH); —, on way down to Hammers, *Rattray 937* (SRGH); —, 15 km E of Inyanga, Mt. Mimunzi, c. 1 900 m, *Bamps, Symoens & vanden Berghen 253* (BR, SRGH); —, Nyamaropa Forest Reserve, c. 3.2 km SE of Muozi, c. 2 130 m, *Simon 653* (LISC, PRE, SRGH); —, Farm "Pamushana", c. 1 830 m (-BD), *Miller 3766* (SRGH); —, Rhodes Inyanga Estate (= "Rhodes Estate", "Inyanga Estate"), c. 1 770–1 830 m, *Hopkins s.n.* sub SRGH 7857 (K, SRGH), *Seagrief 3042* (SRGH), *Whellan 589* (SRGH); —, — and at Pungwe Falls, c. 1 800 m, *Fries, Norlindh & Weimarck 2662* (B, S); —, Rhodes Inyanga National Park, around Fort Nyangwe, c. 2 020 m, *Puff 790124–2/1* (WU); —, —, Fort Hill, *West 4403* (LISC, SRGH); —, —, Mt. Inyangani, c. 1 830–2 580 m, *Bamps, Symoens & vanden Berghen 6* (BR, SRGH), *Chase 3709* (BR, MO, SRGH), 4343 (BM, BR, LISC, MO, PRE, SRGH), *Dale SKF 464* (SRGH), *Fries, Norlindh & Weimarck 3523* (B, SRGH), *Pope 1200* (SRGH), *Puff 790125–1/2a-f* (WU); —, —, "Inyanga Mts.", c. 1 830–2 500 m, *Cecil 203* (K; type of *O. inyangana*), *Humbert 15841* (P); —, —, above bank of Nyamingura R., c. 1 280 m, *Phipps 1260* (SRGH); —, —, Mare R., c. 1 860 m, *Wild 1555* (K, SRGH); —, —, Pungwe River, — Gorge, — View or — Hills, c. 1 170–1 830 m, *Hopkins s.n.* sub SRGH 7176 (K, SRGH), sub SRGH 13118 (BR, K, SRGH), *Rutherford-Smith 518* (MO, SRGH), *Schelppe 582* (BOL, LISC, SRGH), *West 6283* (B, SRGH), *Wild 1481* (K); —, —, Circular Drive between Causeway Cottage and S end of Mt. Inyangani, *Puff 790126–1/1* (WU); Stapleford Forest Reserve, "North Patrol", base of Mt. Ruuinji (-DB), *Puff 790127–2/2* (WU); —, edge of pine plantation near "Dandy's Nek", *Puff 790127–3/3* (WU); Stapleford Forest Station, *Taylor 3287 B* (NBG); — Reserve, c. 1 770 m (-DB or -DD), *Brain 9726* (MO, PRE); Stapleford, *Gilliland 285* (SRGH); Penhalonga (-DC), *Wild 548* (K, SRGH); Umtali Distr., "Mountain Home", *Chase 1209* (SRGH); Umtali, c.

1 580 m, Eyles 1180 (K, SRGH); —, "Cloudlands", c. 1 580 m (-DC or 1932 -BA?), Eyles 5641 (SRGH); Umtali Commonage, "Bideford", Fisher 1430 (NU, PRE), 1436 (SRGH).

—1932 (Melsetter): Vumba Mts., c. 1 520–1 830 m (-BA or -BB), Chase 7299 (MO, SRGH), Corby 270 (SRGH), Craster s.n. sub SRGH 8714 (SRGH), Ferrar 3960 (PRE), Fisher 1120 (NU, SRGH), Garley 117 (SRGH), Greatrex s.n. sub SRGH 14936 (K, SRGH), Hopkins 8052 (SRGH), s.n. sub SRGH 7078 (K, SRGH); —, summit of Castle Beacon, c. 1 900 m (-BA), Puff 790128–1/4 (WU), Corner s.n. (E); —, Leopard Rock, c. 1 750–1 830 m (-BB), Bamps, Symoens & vanden Berghen 690a (BR), Jacobsen 1486 (PRE); Engwa Farm, Himalaya Mts., c. 1 900–1 980 m (-BD), Exell, Mendonça & Wild 122 (LISC, SRGH), Müller 483 (PRE, SRGH); Banti Forest Reserve (-DB), Mavi 491 (B, SRGH); Chimanimani Mts., Martin Forest Reserve, Mavi 685 (BR, SRGH); Melsetter, c. 1 220 m (-DD), Johnson 170 (K), Walters 2726 (K, SRGH); — Distr., Tarka Forest Reserve, c. 1 220 m, Goldsmith 8/68 (B, LISC, MO, PRE, SRGH); "Gazaland", Mt. Pene, c. 2 130 m, Swynnerton 2007 (K).

—1933 (Vila Pery): Chimanimani Mts. (-CC), Goodier 206 (LISC, PRE, SRGH), Thompson 23 (PRE, SRGH); —, Base Camp, Manning CH 25 (SRGH); —, near Outward Bound School, Grosvenor 307 (PRE, SRGH); —, Upper Bundi plain, c. 1 680 m, Hall 230 (SRGH); —, Long Gulley, Noel 2151 (SRGH); —, Stonehenge (Plateau), c. 1 680–1 800 m, Phipps 356, 386 (both PRE, SRGH); —, summit of pass, West 3634 (SRGH); —, summit of Mt. Peza, c. 2 175 m, Goodier 502 (PRE, SRGH).

—2032 (Chipinga): Glencoe Forest Reserve (-BB), Drummond 4974 (BR, PRE, SRGH).

MOÇAMBIQUE—1833 (Vila Gouveia): Barue, Serra de Choa, 10 km from Choa towards border, c. 1 300 m (-AA), Torre & Correia 18626 (LISC); —, —, 21–23 km from (Vila) Gouveia towards border, c. 1 500 m, Torre & Correia 13542, 15462 (both LISC).

—1932 (Melsetter): Manica e Sofala, Tsetsera, 2 140 m, Exell, Mendonça & Wild 237 (BM, LISC, SRGH); —, Serra do Rutanda (-DB), Barbosa 1626 (LISC).

—1933 (Vila Pery): Manica e Sofala, Mavita, Mt. Xiroso (-CA), Mendonça 2628 (LISC); —, Chimanimani Mts., between Skeleton Pass and Camp Portage, c. 1 700 m (-CC), Grosvenor 237 (LISC, MO, PRE, SRGH).

3B. *O. inyangana* subsp. *parvifolia* (Verdc.) Puff, stat. nov.

O. inyangana var. *parvifolia* Verdc. in J. Linn. Soc. Bot. 53: 399 (1950). Type: Zimbabwe (Rhodesia), Chimanimani Mts., Munch 87 (K!, holo.; SRGH!).

Many-stemmed, erect or sprawling perennial herbs or \pm cushion-forming

dwarf shrubs with massive woody bases, c. 10–20 mm in diam., distinctly yellow in cross section. *Stems* few- to \pm much-branched, 100–900 mm long, c. 1,5–2 mm in diam. at the base, c. 0,6–1,5 mm in the mid-stem region; hairs c. 0,1–0,5 (0,8) mm long, in two vertical rows, or stems hairy all over. Longest internodes (2) 7–25 mm. *Leaves* strictly decussate but often appearing whorled owing to presence of well-developed short shoot leaves; *petioles* usually obsolete; blades ascending to spreading, $10\text{--}18 \times 1,6\text{--}3,5$ (4) mm, linear-lanceolate or lanceolate, rarely \pm ovate-lanceolate, glabrous. *Stipular setae* 3 (—5), the longest c. (0,5) 0,8–1,8 mm. *Inflorescences* few- (c. 20-) flowered; head-like, c. (10) 15–20 mm in diam. when in flower, often much elongated, \pm spike-like, up to c. 50 (70) mm long when in fruit. *Buds* claviform. *Flowers* white, pink or mauve; enlarged, foliaceous calyx lobe c. $4,5\text{--}7 \times 0,8\text{--}1,2$ mm, linear-lanceolate or lanceolate, glabrous, setiform lobes c. 0,2–1 mm; *corolla* glabrous outside, throat of corolla and at least upper half of corolla tube a little hairy inside, tube (4) 5,5–9 mm long, narrowly infundibuliform, c. 0,2–0,5 mm in diam. at the base, 0,7–1,5 mm at the throat, lobes (2,5) $3\text{--}4,5 \times 0,6\text{--}1,2$ mm, lanceolate; *filaments* c. 2–4 mm long, sometimes a little hairy near the base, anthers c. $0,5\text{--}0,9 \times 0,3\text{--}0,4$ mm; *style* 9–11 mm, stigma lobes c. (0,4) $0,7\text{--}1,8$ mm, *ovary* c. $0,8\text{--}1 \times 0,5\text{--}0,6$ mm, sparsely to densely covered with hairs $0,1\text{--}0,4$ mm long, the carpel crowned by the enlarged calyx lobe often less hairy than the other. *Fruits* brownish; each mericarp $2\text{--}2,5 \times 0,8\text{--}1$ mm. *Seeds* black, c. $1,3\text{--}1,8 \times 0,4\text{--}0,8$ mm, \pm ovoid, dorsally \pm keeled, ventrally flat.

Chromosome Number: Unknown.

Average Pollen Diameters: 27–31 μm .

Habitat: In open grassland or at the edge of (and sometimes in) scrub, occasionally amongst or around rocks; (presumably) restricted to well-drained sandy soils derived from quartzites (Phipps & Goodier, 1962). Ca. 1 200–1 800 (2 300) m.

Flowering Period: (August) September to June.

Distribution (map, Fig. 10): Endemic to the Chimanimani Mts.

Comments: Subsp. *parvifolia* is distinguished from subsp. *inyangana* and all its “forms” by having always decussately arranged, linear-lanceolate or lanceolate leaves, stems with relatively short internodes and generally fewer-flowered inflorescences.

As far as can be determined from herbarium labels (precise collecting localities and/or ecological notes), subsp. *parvifolia* is confined to quartzite areas, while Chimanimani collections of subsp. *inyangana* seem to originate from areas of schist¹. At least for subsp. *parvifolia*, this is confirmed by the ecological studies of Phipps & Goodier (1962), who state that subsp. *parvifolia* is often co-

¹ Because of the varied geology of the area (cf. Goodier & Phipps, 1962) it is often not possible to determine if a particular collection originated from a schist or quartzite area, even if the collecting locality given is \pm precise.

dominant in higher lying quartzite grasslands. They, however, do not mention subsp. *inyangana*.

Subsp. *parvifolia* and subsp. *inyangana* thus seem to be another example of a pair of vicarious taxa, in which one member is a Chimanimani quartzite endemic; it is comparable to the vicarious species pair *Helichrysum rhodellum* Wild, confined to Chimanimani quartzites, and *H. acervatum* S. Moore, occurring in the Inyangana Mts., the Melsetter Distr. and the Chimanimani Mts., but on Umkondo soils (Wild, 1964).

Since there is a certain amount of overlap in the vegetative characters separating *parvifolia* and *inyangana* (Eyles 8510 from Inyanga, for example, closely approaches *parvifolia*), and since there are no differences in floral and fruit characters (merely the inflorescences tend to differ in extensiveness), *parvifolia* is presently considered a subspecies of *O. inyangana*. I hesitate to elevate *parvifolia* to species rank before the variability of *parvifolia* is studied in the field, and before it is established without doubt that *parvifolia* is in fact confined to quartzite.

COLLECTIONS

ZIMBABWE (RHODESIA)—1932 (Melsetter): Chimanimani Mts., Martin Forest Reserve (-DB), Mavi 621 (LISC, SRGH).

—1933 (Vila Pery): Chimanimani Mts., c. 1 500–2 150 m (-CC), *Bamps*, *Symoens & vanden Berghen* 781 (BR, SRGH), *Guy* s.n. sub SRGH 32 764 (SRGH), *McCosh* 8 (SRGH), *Munch* 87 (K, SRGH; type of ssp. *parvifolia*), *Weiste* s.n. sub SRGH 9121 (SRGH), *West* 3633 (SRGH), *Wild* 2956 (SRGH); —, S approach to higher valley, c. 1 600 m, *Simon* 820 (LISC, PRE, SRGH); —, where upper Bundi leaves plain, ca. 1 600 m, *Phipps* 291 (BR, PRE, SRGH); ± atypical and intermediate to ssp. *inyangana*; —, Long Gully, c. 1 650 m, *Noel* 2150 (SRGH); —, vicinity of Mountain Hut, *Simon* 812 (PRE, SRGH); —, Stonehenge (Plateau), c. 1 700–1 770 m, *Hall* 328 (BOL, SRGH), *Phipps* 358 (SRGH); —, Point 71, *Phipps* 661 (BR, PRE, SRGH); —, immediate vicinity of summit of "Uncontoured Peak", c. 2 300 m, *Goodier* 157 (PRE, SRGH).

MOÇAMBIQUE—1933 (Vila Pery): Chimanimani Mts., E side of Point 71, c. 1 500–2 150 m (-CC), *Hall* 433 (SRGH); —, near Camp Portage, c. 1 600 m, *Simon* 884 (SRGH); —, Martin Falls, *Whellan* 2146 (SRGH); —, unnamed triple falls on tributary below Martin Falls, c. 1 200 m, *Taylor* 1796 (E, NU, SRGH).

4. *O. lanceolata* Verdc. in Garcia de Orta, Sér. Bot. 1: 28 (1973). Type: Moçambique, Manica e Sofala, Makurupini R., c. 5 km from its confluence with Haroni R., E bank, 290 m, *Biegel* 3582 (K!, holo.; BR!, COI, EA, LD, PRE, SRGH!).

Many-stemmed, straggling (sub)shrub. Stems usually much-branched, up to c. 1 m long, c. 1–2 (2,5) mm in diam. in the mid-stem region; hairs c. 0,3–0,8

mm long, in two vertical rows. Longest internodes (20) 35–50 (65) mm. *Leaves* decussate but sometimes appearing whorled owing to presence of well-developed short shoot leaves; petioles obsolete or c. 0.5–1 (1.5) mm; blades spreading to ascending, 23–40 (47) \times 3–6 (7.5) mm, lanceolate or linear-lanceolate, glabrous except for a few short hairs on the margins and midvein above. *Stipular setae* usually 3, c. 0.6–2.5 mm long. *Inflorescences* c. 20- to 30-flowered; head-like, c. 10–20 mm in diam. when in flower, often much elongated, \pm spike-like, up to c. 90 (120) mm long when in fruit. *Buds* claviform. *Flowers* white; enlarged, foliaceous calyx lobe c. 2.5–4 (5) \times 0.3–0.8 mm, \pm lanceolate, glabrous or sometimes with a few hairs on the margins, setiform lobes c. 0.2–1 mm, glabrous; *corolla* glabrous outside, throat of corolla and upper third of corolla tube a little hairy inside, tube (3.2) 3.8–4.5 (5) mm long, narrowly infundibuliform, c. 0.2 mm in diam. at the base, c. 0.8–1.2 mm at the throat, lobes (2.8) 3.2–3.8 \times 0.6–1 mm, \pm lanceolate; *filaments* c. 2.8–3.5 mm long, glabrous, anthers c. 0.6–0.9 \times 0.3–0.5 mm; *style* 6–9 (10.5) mm, stigma lobes c. 0.8–1.5 mm, *ovary* c. 0.7–1 \times 0.5–0.7 mm, \pm densely covered with \pm curled hairs, c. 0.1–0.4 mm long, the carpel crowned by the enlarged calyx lobe sometimes less hairy than the other, occasionally smaller, \pm reduced. *Fruits* brownish; each mericarp 1.5–2 \times (0.4) 0.6–1 mm, the mericarp crowned by the enlarged calyx lobe sometimes without seed. *Seeds* brownish black, c. 1.1–1.3 \times 0.6–0.9 mm, \pm ovoid, dorsally convex, often \pm keeled, ventrally strongly concave.

Chromosome Number: Unknown.

Average Pollen Diameters: 30–30.6 μ m.

Habitat: Usually in wet grassland areas, sometimes on steep (wooded) slopes. Ca. 290–475 m.

Flowering Period: November to January; odd flowering specimens also seen from May, June and August.

Distribution (map, Fig. 10): Endemic to the Haroni-Makurupini area.

Comments: Although closely allied to *O. inyangana*, *O. lanceolata* is easily kept separate by morphological and habitat differences (confined to low altitudes).

The occasional reduction of one carpel (ovule) is not a feature unique to *O. lanceolata* (cf. Verdcourt, 1973), but is also encountered in the other southern African taxa, particularly in *O. cupheoides*.

COLLECTIONS

ZIMBABWE (RHODESIA) and MOÇAMBIQUE. See Verdcourt (1973).

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BOOK REVIEWS

LEHRBUCH DER PFLANZENPHYSIOLOGIE, durch H. Mohr und P. Schopfer, mit xi, 608 Seiten, 639 Abb., und 35 Tab. 3., völlig Neubearb. und erw. Aufl. ISBN 3-540-08739-7. Berlin, Heidelberg, New York: Springer-Verlag, 1978. Gebunden DM 78, US \$39.00. (with pp. xi + 608, 639 figures and 35 tables. 3rd revised and enlarged edition. ISBN 3-540-08739-7. Berlin, Heidelberg, New York: Springer-Verlag, 1978. Cloth DM 78, US \$39.00).

Hans Mohr is a respected German scientist known not only for his research in the field of photomorphogenesis but also for his writings. His books include: *Lectures on Photomorphogenesis* (1972), *Lectures on Structure and Significance of Science* (1977) as well as the predecessor of the volume under review, namely *Lehrbuch der Pflanzenphysiologie* (1969; all published by Springer-Verlag). His latest work, in co-authorship with Peter Schopfer, also of the University of Freiburg, costs about 70% more than did the first edition, so naturally one is interested to know whether, in addition to inflation in the publication industry, this steep price rise might also reflect an increase in scientific content.

Indeed, this attractively-produced book is one-third more voluminous and contains twice as many figures as the first edition. And, I am happy to add, it is a solid, comprehensive text, the kind that should give both teacher and student a framework of conceptual synthesis and integration of the subject of plant physiology. There are 49 chapters which cover the spectrum of plant physiology. As may be expected photomorphogenesis is given strong emphasis but without creating an imbalance as far as other developmental aspects are concerned. The subject matter, based on the curriculum as taught at Freiburg, is innovative, and important and often neglected areas of textbook plant physiology such as for example intracellular morphogenesis, allelochemical reactions, nuclear-cytoplasmic interactions, C_4 /CAM photosynthesis, effects of UV light, rhythms and movements are treated with authority and clarity if in some cases with brevity. With reference to the latter, I refer specifically to cellular recognition systems in plants in conjunction with the role of lectins as well as to the biochemical functions of the higher plant vacuole.

This text is intended for undergraduates but (like *Botany: An Introduction to Plant Biology* by Weier, Stocking and Barbour—John Wiley—which is intended for 1st year students) it is used by post-B.Sc. and doctoral students in preparation for examinations, as well as by teachers as source material. The author citation is substantial and as is usual in a German text the index is detailed.

This text most certainly applies to the teaching and study of plant physiology in southern Africa but unfortunately its usefulness will be limited since few students could be expected to command enough scientific German to warrant its purchase. I see its use as a reference work for teachers of the subject and would hope that an English translation will become available. This should be done as soon as is possible to avoid dating of the information.

There has been a tendency over the past 20 years to assign a number of small texts on specialized plant physiological topics for student course work. In part, this became necessary because of the absence of comprehensive, all-encompassing texts (with few exceptions) in the style of the classic *Introduction to Plant Physiology* by Meyer, Anderson and Böhring; in part, also, because of the feeling that with an ever-expanding subject such as plant physiology a comprehensive text is outdated by the time it lands on the bookseller's shelf. However, plant physiology in recent years has become the junction through which

biochemists and ecologists communicate with each other. *Lehrbuch der Pflanzenphysiologie* also succeeds in putting this aspect into perspective.

CHRIS H. BORNMAN

PLANT HORMONES AND PLANT DEVELOPMENT, by W. P. Jacobs. ISBN 0-521-22062-9. Cambridge: Cambridge University Press, 1979. UK £18.00.

W. P. Jacobs is professor of Biology at Princeton University and one of the pioneers of abscission research. Much of his work on plant hormone-related aspects of abscission has its basis in physioanatomy with the result that his interpretation of functional phenomena are always closely linked to the structural. This, coupled with the fact that he has worked with four major groups of plant hormones, has allowed Jacobs to perceive events in plant growth and development more successfully from the organismal, holistic point of view than those who, for example, have pursued in depth the biochemical and physiological effects of but one or at most two hormones.

This book, intended for advanced under-graduate as well as post-graduate students, consequently reflects a rich and varied experience with all the plant hormones except ethylene, and if—as the author himself readily admits—it lacks the detailed depth of a life-time's activities with one hormone, it succeeds in providing balance and synthesis of the role of four of the five groups of hormones that in one way or another control and co-ordinate plant growth and development.

Since the author also holds the philosophy that it is just as important to describe the development of research ideas as it is to describe the development of plants, students of hormone physiology will find his critical analysis of some of the hundreds of experiments (ca. 900 references are cited) under review a startling reminder of how essential it is that scientific research be well planned.

A large part of the book is devoted to the auxins. The gibberellins are mainly reviewed in conjunction with the "flowering hormones" but, with the cytokinins and abscisic acid, are critically appraised. Of the 11 chapters, the two dealing with movement and roots are of particular interest, especially the latter since in the author's view root development is one of the research areas of greatest importance in our current state of ignorance. The last chapter is an overview in which the author assesses the present status of plant hormone knowledge from the organismal point of view, lending flavour with cryptic interpretations to the results of many of the well-known experiments.

The major weakness of this book is in relation to ethylene. It is barely mentioned. Could it be that the author does not share the view that this ubiquitous gas with its profound physiological and biochemical effects qualifies it as a plant hormone in the classical sense? Or does its absence simply reflect the fact that it was not part of the stable of plant growth regulators upon which Jacobs and co-workers focused their attention? I assume, since this book is based more on personal than collective experience, that it is the latter.

CHRIS H. BORNMAN

BIOCHEMISTRY AND PHYSIOLOGY OF PLANT HORMONES, by T. C. Moore, with pp. xii + 274, 164 figures and 13 tables. ISBN 3-540-90401-8 (Berlin, Heidelberg), ISBN 0-387-90401-8 (New York). Berlin, Heidelberg, New York: Springer-Verlag, 1979. Cloth DM 49, approx. US \$27.00, UK £12.15.

Most students interested in and working on problems related to plant growth regulators will welcome the appearance of this book. It is written by someone who not only himself has been intensively involved in plant hormone research (auxins and gibberellins), but who also has had considerable experience in teaching this aspect of plant physiology

to post-graduate students. In fact, I suspect this book is based on lecture material used in theoretical and practical courses in plant hormone physiology.

The book consists of 7 chapters, 5 of which are devoted to the five major groups of plant hormones, namely auxins, gibberellins, cytokinins, abscisic acid and ethylene. The first chapter introduces terminology and concepts, gives a review of the phenomenon of growth and the mechanisms that control cellular differentiation, and hints at the regulatory role of plant hormones in growth and development. The seventh and last chapter deals not with a hormone, but with the pigment phytochrome. Phytochrome is also very intimately involved in the control of a plant's growth and developmental history and as there are a number of critical interactions between this pigment system with hormone metabolism and action, it is not illogical to explore the connection.

The chapters on the various hormones provide interesting facts on their discoveries, occurrences, chemical characteristics, physiological and biochemical effects, synthesis, metabolism and modes of action, etc. The book as a whole provides basic information in a logical and stepwise fashion that cannot but aid the student in developing an integrated understanding of this complex (in the words of the misinformed: "mixed up") field of plant physiology.

Students of botany and of its applied fields such as crop science, horticulture, pasture science, and forestry should find this clearly and concisely written treatise very useful.

CHRIS H. BORNMAN

ORGANIZATION IN PLANTS, by W. M. M. Baron, with pp. iii + 264, 163 figures and 25 tables. 3rd edition. ISBN 0-7131-2643-A. London: Edward Arnold, 1979. Paper R16.90.

This third edition succeeds the fourth reprint of the previous edition and has been extensively modified, updated and adapted to particularly emphasize the whole plant in relation to its surroundings. In the author's own words the main aim was to: "bring out ways in which the plant interacts with its environment and so is able to compete successfully with its neighbours". At a time when progressively more emphasis is being placed on the ecophysiological approach to plant growth, the author has admirably succeeded in integrating growth and development with the plant's surroundings.

The text is directed at the introductory courses to a study of plant physiology and consequently aims to explain the various processes in plants in an easily comprehensible way. Structure is skilfully integrated with function.

A very useful feature of this book is the frequent reference to experimental procedures to back up the more theoretical discussions. This serves to emphasize the experimental nature of plant physiology and stimulates the reader to critical thought. In an appendix 64 experiments are grouped together to supplement the different chapters. Description of experiments are concise and directly related to the text.

In eight chapters cell organization, water relations, photosynthesis, respiration, mineral nutrition, biochemistry of cell activities, co-ordination in the plant and the physiological organization and life cycle of plants are profusely illustrated by graphs, electron micrographs, photographs and line drawings eliciting the text even further.

J. H. VISSER

PERSPECTIVES IN GRASSLAND ECOLOGY, edited by Norman French, with pp. 204 + xi, 60 figures and 47 tables. Volume 32 in the series "Ecological Studies". Berlin, Heidelberg, New York: Springer-Verlag, 1979. DM 54.

The book is bound neatly in a hard cover of 165 × 240 mm in size. Good quality paper is used and the letter printing is of a high standard. Different type sizes have been em-

ployed without creating an imbalanced effect. Italics have been used for the scientific names and mathematical formulae.

A list of contributors responsible for the text, as well as their present addresses is given in the preliminary pages of the book. Each chapter contains an introduction, methods of analysis, results, summary and a list of references. A particularly valuable feature is the adequate lists of references to literature, much of which may not be familiar to every grassland ecologist.

The purpose of this book is to present a summary of quantitative ecological investigation of North American grasslands and to present a set of broad comparisons of their characteristics and functions as well as the results of some models and experiments that lead to practical considerations of the management of grasslands.

Following the introduction, in which the types and general characteristics of North American grasslands are presented, there are ten chapters which focus on general categories of grassland ecosystem studies:

- (i) primary production and factors controlling it,
- (ii) the effects of aboveground and belowground consumers in the grassland ecosystems,
- (iii) nutrient cycling and the application of simulation modelling in grasslands and
- (iv) the most important subsystem interactions in grasslands.

In this book the current concepts of grassland ecosystem structure and function are clearly presented and could also be applicable to South African conditions.

The illustrative matter is of a good quality, accurately presented and relevant to the text. The subject index at the back of the book is comprehensive and detailed but unfortunately an author index is not presented.

This well-produced book is highly recommended for botanists and pastoralists interested in grassland ecosystem ecology from both teaching and research points of view.

W. L. J. VAN RENSBURG

THE *ALOINEAE*, A BIOSYSTEMATIC SURVEY, by H. P. Riley and S. K. Majumdar, with pp. x + 180, illustrations. ISBN 0-8131-1376-8. University Press of Kentucky, 1979. R28,75.

The book is a scholarly treatment of the biosystematics of the *Aloineae* which can certainly be recommended to those with a research interest in the tribe, and to some extent to students of biosystematics in general.

Apart from short sections on chromatography, ultrastructure and related studies, the book is essentially concerned with chromosomes. Given that the lesson of the chromosomal constancy of the tribe may well be that ecological factors are probably of major importance in the maintenance of species integrity, it is therefore unfortunate that, for example, flowering time as an isolation mechanism does not find a mention. Moreover, given that a work of this size is devoted primarily to the chromosome cytology of an extremely uniform group it is perhaps predictable that much of the work is a description of the historical development of the subject, which detracts from the elements of dynamism and synthesis to be hoped for in a book promising such a modern approach. The result is that certain sections are boring; and the same can be said of the chapter on species distribution which, although very complete, becomes unreadable to the point of absurdity as the authors introduce into the text long lists of species names which probably mean little to most readers and could have far better been tabulated.

One might have hoped, for instance, that some definite indication be provided of the genetical significance of the bimodal karyotype; its possible function as the provision of two recombination systems is hinted at, but never firmly asserted. Similarly, a work of this size could have described the inter-tribal linkages provided by the bimodal karyotype, an important and interesting field which Darlington found time for in his much more general *Chromosome Botany*.

The book is well produced and free of errors, though "self-pollination" on p. 146 should presumably read "cross-pollination". The use of photographs and idiograms rather than camera lucida drawings is to be commended, though one wishes that chromosomes in idiograms could be provided with straight sides (Fig. 4.4) and that translocations, where they are illustrated by photographs, be indicated by arrows where not immediately obvious (Fig. 9.2).

The book is a valuable reference work, and the detailed descriptions of certain aspects of cytology, such as E-type bridges, make informative reading even to accomplished cytologists. It is strange, however, that chromosome banding is not thought worthy of mention. Admittedly, few such studies have been made in the *Aloineae*, but the authors' own illustration of cold-sensitive segments in *Haworthia* point to their likely importance.

The book will have succeeded if it helps point the way to a new breed of biosystematic treatments based on the precept that, where chromosomal differences can be detected, they constitute a firm indication of whether two taxa interbreed and therefore, in the evolutionary sense, constitute separate species. As such, the book is both encouraging and stimulating; encouraging by virtue of championing the role of cytotaxonomy to a taxonomic audience to which it is still constantly necessary to argue the value of chromosomes, and stimulating by virtue of reminding us of the vast potential for cytotaxonomy existing at our doorstep. The book serves to emphasise the continued reliance of South African cytotaxonomy on the occasional visits of overseas experts, but by doing so it may perhaps serve a corrective role.

D. J. MOGFORD

SCANNING ELECTRON MICROSCOPE STUDIES OF THE LEAF EPIDERMIS IN SOME SUCCULENTS, by D. F. Cutler and Heidrun Hartman, with pp. 50 + iv, 15 plates (77 photographs) and 18 references. Wiesbaden: Franz Steiner Verlag GmbH, 1979. DM 17.80.

The booklet represents pages 447–497 of vol. 28 of "Tropische und subtropische Pflanzenwelt" which is edited by W. Rauh. It contains two chapters. The first by Cutler is entitled: "Leaf surface studies in *Aloe* and *Haworthia* species (Liliaceae): Taxonomic implications". It deals with sixteen *Haworthia* and eleven *Aloe* species.

Although the descriptions that are provided were derived from only one specimen of each species, the author is convinced that . . . "it is highly probable that they (the descriptions) will be accurate in most respects for other samples" because it has been established that the characteristics that are described are under strong genetic control. The specimens that were studied were all from the research collection at Kew.

In general, it was found that M. B. Bayer's recent revision of *Haworthia* is well supported at the subgeneric level by the results. The very small number of *Aloe* species that were examined severely restricts the taxonomic value of the work on this genus.

In the second chapter of the booklet, Hartman deals with "Surface structures of leaves: their ecological and taxonomical significance in members of the subfamily Ruschioideae Schw. (Mesembryanthemaceae Fenzl)".

Most of the material that was examined was collected by the author during two excursions to South Africa. Fifty-four species (*Cheiridopsis*, 10; *Cephalophyllum*, 18; *Fenestraria*, 1; *Leipoldtia*, 7; *Octopoma*, 6; *Ottosonderia*, 1; *Schlechteranthus*, 2; and *Vanzijlia*, 1) were examined. The sections were air-dried as it was found that drying by the critical point method results in the dissolution of the epicuticular wax layers. In this respect the leaves of members of the Ruschioideae appear to differ from those of species of *Aloe* and the Mesembryanthemoideae.

Although the English of the second chapter could have been improved somewhat, both chapters are written in a concise but clear way. The main appeal of the work will undoubtedly be its many illustrations which in most cases were prepared with the help of

a scanning electron microscope. The booklet should be of value mainly to researchers and post-graduate students of morphology and taxonomy.

N. GROBBELAAR

DIE INFLORESZENZEN DER HYDROCOTYLOIDEEN (APIACEAE), deur Hans A. Broebe, met pp. 181 en 57 figure. Wiesbaden: Franz Steiner Verlag GmbH (Tropische und subtropische Pflanzenwelt, 29). DM 71,80.

Volgens Engler & Prantl (*Planzenfam.* 1898) is die Hydrocotyloideae 'n subfamilie van die familie Umbelliferae. Hieruit is dit duidelik dat die werk van Froebe wat oor die bloeiwyses van verteenwoordigers van 37 genusse van die Hydrocotyloideae handel 'n gespesialiseerde publikasie is wat hoofsaaklik op navorsingswerkers en nagraadse studente toegespits is. Vir planttaksonomie en morfoloë is die werk van groot belang aangesien die outeur nie alleen daarin slaag om verskillende tipes bloeiwyses in die groep te identifiseer en beskryf nie maar slaag hy ook daarin om interessante filogenetiese reekse waar te neem. Interessant hier is ook die feit dat die outeur die terminologie wat Troll en Weberling vir bloeiwyses voorgestel het, gebruik het aangesien die terminologie nie algemeen gebruik word nie.

In die teks word die bloeiwyses van 37 genusse beskryf en deur middel van 57 figure pragtig geïllustreer. Vier van die 37 genusse word in Suidelike Afrika verteenwoordig. Die figure behels nie alleen sketse van die bloeiwyses nie maar ook skematiese voorstellings en grondplanne daarvan. Die feit dat die outeur deurgaans van gestandaardiseerde simbole gebruik maak vergemaklik die interpretering van die figure en lei ook daartoe dat bloeiwyses van verskillende spesies maklik vergelyk kan word.

Van die 37 genusse onder bespreking is feitlik alle spesies bestudeer. Aan die einde van die teks word 'n lys van alle bestudeerde eksemplare met die name van die versamelaars asook die name van die herbariums waar die eksemplare geberg word voorsien. Ook word 'n lys van geldige en ongeldige name gegee wat moontlike verwarring uit-skakel.

Die publikasie wat in Q1 formaat op duursame glanspapier gedruk is, kan voorwaar vir navorsers op hierdie gebied aanbeveel word.

W. F. REYNEKE

CUTICULAR-TAXONOMIE DER GRÄSER EINES WEST-AFRIKANISCHEN SAVANNEN GEBIETES UNTER DEM ASPEKT DER FUTTERPRÄFERENZ-ANALYSE WILDLIBENDER GROBSAUGER, deur Wilhelm Barthlott en Brigitta Martens, met pp. 113 en 71 figure. Wiesbaden: Franz Steiner Verlag GmbH (Tropische und subtropische Pflanzenwelt 30, 1979). DM 38.

Hierdie publikasie handel in hoofsaak oor die bou van die blaarepidermis van 40 grasspesies, wat in 25 genusse resorteer, wat in die Camoé Nasionale Park (Noordelike Ivoorkus) voorkom.

In die twee inleidende hoofstukke word die agtergrond waarteen die navorsing onderneem is en 'n beskrywing van die plantegroei van die gebied gegee. Daarna volg 'n volledige bespreking van die metodes en terminologie wat gebruik is. Aangesien daar min van die bestaande terminologie afgewyk word, behoort die leser min moeite met die interpretering van die teks en figure te onervind.

'n Sleutel waarvolgens die ondersoekte spesies van mekaar onderskei kan word, word voorsien. Slegs twee spesies van die genus *Loudetia* en twee van die genus *Andropogon* kan nie van mekaar onderskei word nie. Die beskrywings van die epidermis van die spesies is in telegramstyl en die aandag is hoofsaaklik op die abaksiale epidermis toegespits. Die beskrywings gaan in die meeste gevalle gepaard met lyntekeninge wat deurgaans op

die bladsy teenoor die beskrywing voorkom en dus die rondblaaï op soek na figure uit-skakel. In enkele gevalle word ook van fotomikrograwe gebruik gemaak terwyl daar ook ses aftaselektronmikrograwe verskyn.

Alhoewel die outeurs vermeld dat die verskillende soorte op verskillende tye van die jaar en in verskillende habitate ondersoek is, bestaan daar onduidelikheid in verband met die metodes waarvolgens die variasie binne 'n soort bestudeer is. Die outeurs kom dan ook tot die ietwat vreemde gevolgtrekking dat die variasie binne 'n spesie primêr afhanklik is en beïnvloed word deur lugvogtigheid en dat die variasie as gevolg van die habitat minimaal is en nie die identifisering van die soorte beïnvloed nie.

Slegs tien van die ondersoekte spesies word in Suidelike Afrika aangetref en om dié rede sal die publikasie 'n beperkte gebruik in Suid-Afrika ondervind. Die publikasie lewer egter 'n betekenisvolle bydrae tot die kennis van die bou van die epidermis van grasse oor die algemeen en sal dus met vrug deur navorsers gebruik kan word.

Die publikasie is in Q1 formaat op duursame glanspapier gedruk en die tekeninge, fotomikrograwe en aftaselektronmikrograwe is van besonder hoë standaard.

P. D. F. Kok

BROMELIENSTUDIEN: 1. NEUE UND WENIG BEKANNTE ARTEN AUS PERU UND ANDEREN LÄNDERN, deur Werner Rauh, met pp. 29 en 15 figure. Wiesbaden: Franz Steiner Verlag GmbH (Tropische und subtropische Pflanzenwelt 31, 1979). DM 10,60.

Soos die subtitel van die publikasie aandui word in die teks nuwe en skaars taksons in die familie Bromeliaceae beskryf. Die betrokke taksons ressorteer onder vier genusse naamlik *Tillandsia*, *Gusmania*, *Fosterella* en *Vriesea*. In eersgenoemde genus word drie nuwe spesies en een variëteit beskryf terwyl na een skaars spesie verwys word. In die genus *Gusmania* word een nuwe spesie en een variëteit en in laasgenoemde twee genusse elk een spesie beskryf. Met die uitsondering van twee van die nuut beskryfde taksons het die outeur van die publikasie al die ander taksons beskryf.

Die beskrywings behels die latynse frase gepaardgaande met die verwysing na die holotipes en die verspreiding van die takson. Geen verspreidingskaarte word egter voorsien nie. Elkeen van die beskrywings is vergesel van twee foto's waardeur die meeste kenmerke van die taksons duidelik geïllustreer word. By een van die taksons word ook van tekeninge gebruik gemaak. Beskrywings van die taksons in Duits word ook voorsien.

Geeneen van die taksons wat beskryf word, word in Suid-Afrika aangetref nie en daarom is die publikasie vir die deursnee Suid-Afrikaanse plantkundige van relatief min belang. Vir taksonome in die familie Bromeliaceae en spesifiek die betrokke vier genusse, is die werk egter van groot belang.

Die publikasie is in Q1 formaat op duursame glanspapier gedruk en die foto's en tekeninge is van 'n hoë standaard.

P. D. F. Kok



TAXONOMIC STUDIES ON THE *DISINAE*: 2. A REVISION OF THE GENUS *SCHIZODIUM* LINDL.

H. P. LINDER

(*Bolus Herbarium, University of Cape Town*)

ABSTRACT

The genus *Schizodium* is revised. Six species and two subspecies are recognized. Notes on the taxonomically important morphological characters are given. The available information on the ecology and distribution of the taxa is discussed.

ERRATUM

SIENING VAN

Vol. 47 (2) : 195 - 212. Observations on the effects of fire in mountain fynbos at Zachariashoek, Paarl, by B. W. van Wilgen and F. J. Kruger.

Page 200 Table 2: the heading of Frequency % should read Frequency, number of plots.

ord erken. Aangegee. Die bespreek.

INTRODUCTION

Schizodium, a genus of six species, is one of the more peculiar members of the subtribe *Disinae*. This report is part of a general taxonomic study of the whole subtribe.

This genus is one of the first Cape genera to be comprehensively known: by 1838 all the species had been described. Two species were described by Linnaeus (1760), and one by Thunberg (1794). Lindley (1838) described the remaining three species. Lindley also circumscribed the genus as it is understood today.

Subsequent to 1838 several more species were proposed. Bolus transferred the genus to *Disa* in 1888. The genus was revised by Kraenzlin (1900), Schlechter (1901) and Rolfe (1913). Kraenzlin and Rolfe essentially followed Lindley's treatment. Rolfe, by applying the "Kew Rule" even perpetuated Lindley's nomenclatural errors. Schlechter radically redefined the specific boundaries in the genus, to form groups approximating those proposed in the present work. This similarity in treatments is obscured by Schlechter's misapplication of the

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UITTREKSEL

TAKSONOMIESE ONDERSOEK VAN DIE *DISINAE*: 2. 'N HERSIENING VAN DIE GENUS *SCHIZODIUM* LINDL.

Die genus *Schizodium* word hersien. Ses spesies en twee sub-spesies word erken. Aantekeninge oor die taksonomies belangrike morfologiese karakters word gegee. Die beskikbare informasie oor die uitbreiding en ekologie van die taksa word bespreek.

INTRODUCTION

Schizodium, a genus of six species, is one of the more peculiar members of the subtribe *Disinae*. This report is part of a general taxonomic study of the whole subtribe.

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name *S. bifidum* (Thunb.) Reichb. f. to *S. obliquum* Lindl., and by his dividing *S. longipetalum* Lindl. into *S. antenniferum* Schltr., based on a single collection, and the rest of *S. longipetalum*, which he included in *S. bifidum*. The nomenclatural errors of the Schlechter and Rolfe treatments, plus the uncritical treatment by Rolfe (who recognized eight species), resulted in some confusion.

NOTES ON MORPHOLOGY

Vegetative morphology

The distribution and structure of the leaves are uniform throughout the genus. The basal leaf margins are crisped in *S. longipetalum* and sometimes in *S. inflexum* and *S. bifidum*. In general the leaves are concolorous green on the upper surface, but often they are purple below. Towards the eastern part of the distribution range of *S. inflexum* two parallel lines of purple spots frequently appear on the upper surface.

In all species except *S. flexuosum*, *S. bifidum* and *S. inflexum* the stems are strongly flexuose, with at least two 90° angles at right angles to one another. In the three exceptions the angles are often less than 45° and may even be completely absent.

Sepals

The sepals are subequal. Three general shapes are found: in *S. flexuosum* the lateral sepals are broadly obovate. In *S. bifidum*, *S. inflexum* and *S. obliquum* the lateral sepals are narrowly lanceolate, acute and spreading. The other extreme is found in *S. cornutum* and *S. longipetalum*, in which the sepals are narrowly lanceolate and acuminate, and frequently recurved. The most extreme expression of this is found in Schlechter 5248.

Spur

Spur characters have great taxonomic value, but are often difficult to interpret on dried material. In *S. obliquum* the spur is dorsoventrally constricted, and in *S. inflexum* it is widened at the base. The other taxa occupy intermediate positions. Spur length is too variable to provide a good character. The direction of the curvature of the spur can provide valuable information, but exceptions occur.

Petals

The petals consist of a narrowly oblong to lorate limb, which is geniculately upcurved, a basal anticus process and a bifid apex. The limb varies among the species, but the other two characters are valuable. The basal anticus process may be absent (*S. flexuosum*, *S. longipetalum*), developed as a fold (*S. bifidum*, *S. inflexum*), or as a lobe (*S. obliquum*, *S. cornutum*). The bifid apex can be

suppressed, or be equally bifid, or the anterior tooth can be greatly elongate as a filiform tooth (*S. longipetalum*).

Lip

The lip is the most distinctive organ in the genus, and is elaborated into three parts:

1. An apical tooth, which is subulate in all the taxa except *S. flexuosum*, where it is wedge-shaped. Vogel (1959) refers to this as the epichile. Even though the length of the tooth can be variable in some populations, it shows a strong correlation with the specific groupings, being relatively short in *S. obliquum*, intermediate in the *S. longipetalum*.
2. The central horizontal portion (mesochile) is not very variable. In *S. flexuosum* it is yellow with almost black spots, while in the other taxa it is more or less pale pink with parallel lines of dark purple spots. The margin may be plane or undulate.
3. The basal erect concave part (hypochile) of the lip hardly varies among the taxa.

Gynostegium

This structure is remarkably uniform within the genus. The anther is borne horizontally. The rostellum is vertical, and in most species the lateral lobes are well developed and horn-shaped, bearing the viscidia, while the central lobe is reduced to a small fleshy blob between the lateral lobes. In *S. longipetalum* the central lobe is developed as a small flap which lies on the anther. The stigma is shortly pedicellate, the stigmatic surface horizontal, almost oblong, with two well developed cushions and one small cushion.

TAXONOMY

Schizodium Lindl.

Leaves in a flat basal rosette; stem wiry, generally flexuose, less than 400 mm tall; petals erect, bifid apically, lip pandurate, apical part tooth-like, pendant; middle part flat; basal part erect, concave, closing the entrance to the spur; flowers white to pink, in one species yellow.

Plants herbaceous; tubers testicular to globular, c. 10 mm in diameter; stem annual, 60–400 mm tall, wiry flexuous, pale green to purple. *Leaves* basal and cauline; basal leaves in a flat rosette, 3–10, petiolate, spatulate to lorate, apiculate, margins flat or undulate, up to 25 mm long; cauline leaves 1–4, lanceolate, obtuse to acuminate, the apical part usually free.

Inflorescence 1–8 flowered, lax; bracts similar to the cauline leaves; pedicels often distinct from the ovary, included in or exerted from the bracts. *Dorsal sepal* superior, narrowly lanceolate to broadly obovate, obtuse to acuminate, usually galeate; spur 2–12 mm long, acute to bifid, straight or decurved or up-curved, horizontal at the base; linear or clavate, often dorsoventrally constricted at the base. *Lateral sepals* narrowly lanceolate to broadly obovate, obtuse to acuminate, 5–18 mm long. *Petals* free, vertical, usually narrowly oblong, zygomorphic with a posterior knee-bend, apex equally or unequally bifid, sometimes with the anterior tooth long and subulate, basal anticus lobe usually present. *Lip* pandurate; apical tooth wedge-shaped or subulate, 2–16 mm long, pendant or reflexed; mesochile flat, horizontal, broad, the margins occasionally undulate; hypochile vertical, concave, pale, closing the entrance to spur. *Column* short; anther horizontal; rostellum lateral lobes well developed, erect, the apices enclosing the globular viscidia; stigma horizontal, three-cushioned, shortly stipitate.

NOMENCLATURE AND TYPIFICATION

Schizodium Lindl. in Gen. Sp. Orch.: 358 (1838); Harv. in Gen. Pl. ed. 2: 366 (1868); Benth. & Hook. f. in Gen. Pl. 3: 631 (1831); Pfitzer in Nat. Pfl. Fam. 2. 6: 97 (1889); Dur. & Schinz in Consp. Fl. Afr. 5: 113 (1892); Kraenzl. in Orch. Gen. Sp. 1: 723 (1900); Schltr. in Bot. Jahrb. 31: 299 (1901); Rolfe in Fl. Cap. 5. 3: 253 (1913). Schltr. in Die Orchideen: 275 (1915); Senghas in Schltr., Die Orchideen; 275 (1974); Dyer in Gen. S. Afr. Fl. Pl. 2: 993 (1976). *Disa* Bolus in J. Linn. Soc. 25: 196 (1889).

Type: *Schizodium flexuosum* (L.) Lindl., basionym: *Orchis flexuosa* L.

ETYMOLOGY

Probably from the Greek: Schizein = split, eidos = similarity to; referring to the bifid petals (Schultes & Pease, 1963).

KEY TO THE SPECIES OF *SCHIZODIUM*

1. Sepals ovate; dorsal sepal convex, not galeate: 1. **flexuosum**
 1. Sepals lanceolate to linear; dorsal sepal concave, galeate
 2. Sepals obtuse to acute, not reflexed or recurved
 3. Anticus process of the petal a large lobe, often with a serrate upper margin; spur dorsoventrally constricted at the base
 4. Lateral sepals usually longer than 8,5 mm; from the Cape Peninsula, Cape Hangklip, and the flats from the Peninsula to Darling: 4a. **obliquum** ssp. **obliquum**
 - 4'. Lateral sepals usually shorter than 8,5 mm; not from the above areas: 4b. **obliquum** ssp. **clavigerum**

- 3'. Anticous process a small fold; base of the spur widened
 - 5. Dorsal sepal 3–6 mm wide; spur generally slender and curved upwards: 2. **bifidum**
 - 5'. Dorsal sepal 2–3.5 mm wide; spur thick and generally straight or curved downwards: 3. **inflexum**
- 2'. Sepals acuminate, reflexed or recurved
 - 6. Anticous lobe small; petal without a long filiform tooth: 5. **cornutum**
 - 6'. Anticous process absent; petal with a filiform tooth at least as long as the petal: 6. **longipetalum**

1. *Schizodium flexuosum* (L.) Lindl.

Sepals obovate; dorsal sepal erect, concave, reflexed; spur decurved, bifid; flowers brightly white and yellow coloured.

Plants erect, flexuose, 150–350 mm tall, stem pale green to purple, nitid. *Leaves* basal and cauline; basal leaves petiolate, oblanceolate to spatulate, 10–20 mm long and 5–9 mm wide, petiole linear, often sheathing the stem, 5–15 mm long; cauline leaves 2–6, oblanceolate, acute to obtuse, 10–20 mm long, the upper $\frac{2}{3}$ free and recurved from the scape. *Inflorescence* (1)–3–(5) flowered; bracts like cauline leaves; pedicels 5–8 mm long, not exerted from the bracts, ovaries 5–10 mm long; flowers with white sepals and yellow petals and lip, the latter with black spots. *Dorsal sepal* obovate to broadly obovate, 7–10 mm long and 5–10 mm wide, concave, erect with the margins reflexed; spur 2–4 mm long, sharply bent downwards, apex bifid. *Lateral sepals* obovate to broadly obovate, 7–11 mm long and 4–9 mm wide. *Petals* 3–5 mm long, anticous lobe absent, apex bifid, the front tooth as long as the limb, narrowly linear, rarely subulate, the rear tooth very reduced or absent, not included in the galea. *Lip* tripartite; apical tooth wedge-shaped, acute, the margin strongly undulate, 2–4 mm long; mesochile 3–7 mm wide, the margins strongly undulate; hypochile small, concave. *Column* short, anther reflexed, rostellum erect, minute.

NOMENCLATURE AND TYPIFICATION

Schizodium flexuosum (L.) Lindl. in Gen. Sp. Orch.: 359 (1838); Kraenzl. in Orch. Gen. Sp. 1: 726 (1900); Rolfe in Fl. Cap. 5, 3: 254 (1913).

Orchis flexuosa L. in Pl. Rar. Afr.: 26 (1760). Type: *Oldenland* in Herb. Burman (G!, holotype).

Satyrium flexuosum (L.) Thunb. in Prod. Pl. Cap.: 5 (1794).

Disa flexuosa (L.) Sw. in Kongl. Vet. Acad. Handl.: 212 (1800); H. Bol. in Trans. phil. Soc. S. Afr. 3: 160 (1888).

Icones: H. Bolus, Icones Orch. Austro-Afr. 2: t.92 (1911). Schelpe, An introduction to the South African orchids, Pl. 52 (1966). Mason, Western Cape Sandveld Flowers, Pl. 37.3 (1972).

The first collections of this species were apparently made by Oldenland, who was a gardener at the Cape between about 1695 and 1699, when he died. He sent dried material to several people, including Petiver in England. Eventually part of his herbarium fell into the hands of the Burman family (Karsten, 1951). N. L. Burman took this collection to Carl von Linné in the summer of 1760, when the eminent botanist described *Orchis flexuosa* from an Oldenland collection. The Burman herbarium is now in Geneva where the type of *O. flexuosa* still is.

On the type sheet are several annotations, including one indicating that Oldenland was the collector of the specimen, and one referring to Ray's monumental *Historia Plantarum* Tome 3 page 586. Here Ray described an *Orchis Africana*, *nudi hominis effigiem referens*, collected by Oldenland, in Museum Petiver 281. A short description follows, which contains no elements contradicting the description of *S. flexuosum*. It is therefore possible, but by no means certain, that this citation does refer to *S. flexuosum*.

Linnaeus the Younger described *Orchis flexuosus* (1781) from a Sparrman collection: this is a mixed collection of *S. flexuosum* and *S. obliquum* ssp. *obliquum*. Lamarck (1796) also refers to *S. flexuosum*, but under the name of *Orchis undulata*.

DISTRIBUTION AND ECOLOGY

This species falls into the Western Group as defined by Weimarck (1941), with a distribution area extending from Nieuwoudtville to the Caledon Swartberg (Fig. 2). There is also an outlier population at Darling. In view of this, its absence from the Piketberg is remarkable.

It is usually associated with an ericoid—restioid dominated vegetation on alluvial sand derived from Table Mountain Sandstone along streams and in moist spring conditions. A few populations have also been found on shallower soils, but not on mountain slopes. With a few exceptions, all localities are below 1 000 m, and range to near sea-level.

Almost all the precipitation in the area is restricted to the winter months, and ranges from about 500 mm p.a. to about 1 000 mm p.a. (W.B. 29). In some localities snow occurs occasionally in winter.

This species is commonly known as "Salt and Pepper" or "Bacon and Eggs".

REPRESENTATIVE COLLECTIONS

Paarl, in sandy depressions near Paarl, *MacOwan & Bolus* 172 (BM, G, GRA, K, P, UPS, ZT); Vanrhynsdorp, Gift Berg, Sept., *Phillips* 7561 (BOL, K, PRE, SAM, STE); Malmesbury, between Malmesbury and Groenekloof, in damp sand, Oct., *Bolus* 4332 (BM, BOL, K, Z).

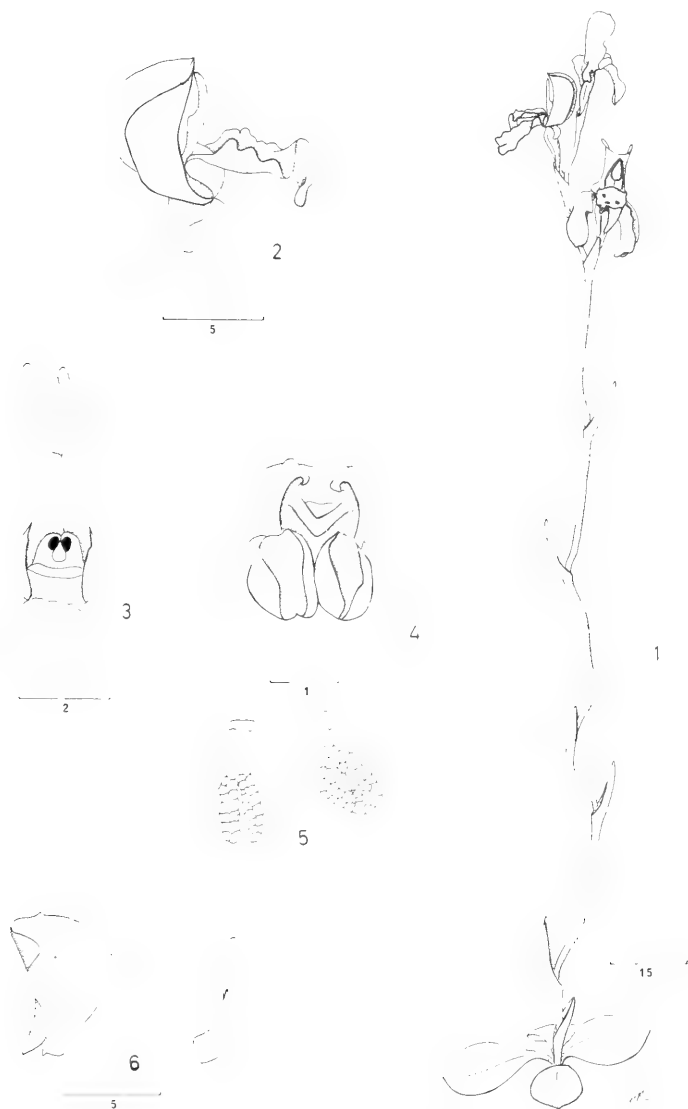
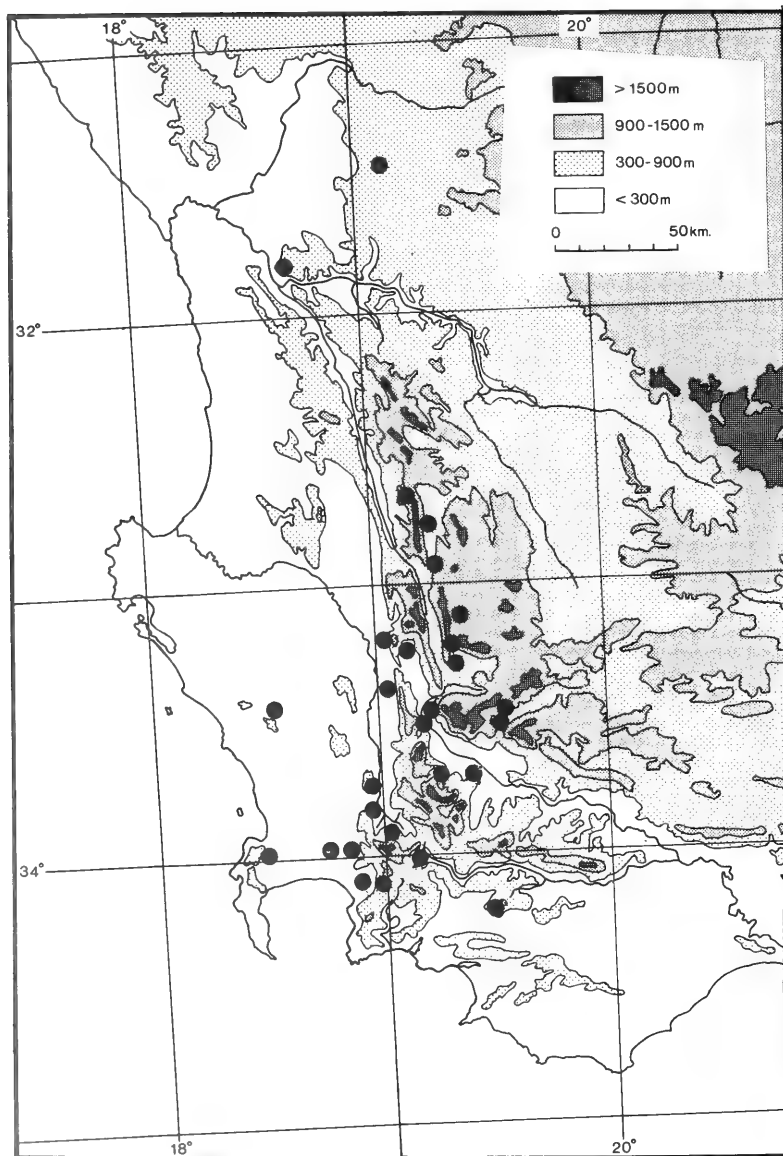


FIG. 1.

S. flexuosum (from Linder). 1. Whole plant, 2. Flower without lateral sepals, 3. Front view of petals and column, 4. Rear view of rostellum, 5. Pollinaria, 6. Sepal and petal in 3 dimensions.



G.P.-S. (L).

FIG. 2.
Distribution map of *S. flexuosum*.

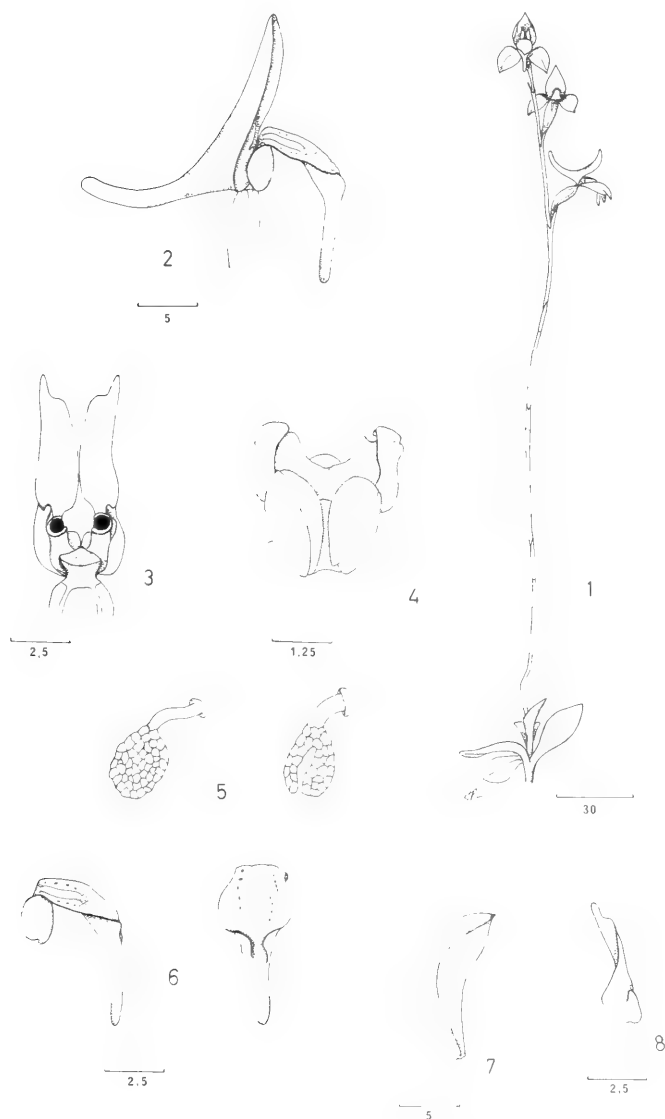


FIG. 3.

S. bifidum (from *Linder*). 1. Whole plant. 2. Flower with lateral sepals removed. 3. Front view, showing petals and column. 4. Rear view of the rostellum. 5. Pollinaria. 6. Lip. 3-dimensional views. 7. Lateral sepal. 8. Petal.

2. *Schizodium bifidum* (Thunb.) Reichb. f.

Petals with a basal anticous fold; lateral sepals 9–17 mm long and 2.5–4.2 mm wide; spur base in line with the base of the dorsal sepal, generally curved up and narrowed to a point.

Plants straight or sub-flexuose, stem wiry, nitid. *Leaves* basal and cauline; basal leaves spreading, petiolate, the blade narrowly obovate, apiculate, 10–20 mm long and 5–10 mm wide, the margins often undulate, the upper surface occasionally with purple spots; cauline leaves distant, lax, lanceolate, acute to acuminate, 1–5, 6–16 mm long. *Inflorescence* 1–7 flowered; bracts similar to the cauline leaves; pedicels 2–11 mm long, rarely exerted from the bracts, ovaries 3–11 mm long; flowers more or less pink, sepals with small purple freckles on the backs along the midvein, lip tooth greenish to purple, mesochile of the lip with purple spots on the upper surface, apex of the petals often darker. *Dorsal sepal* erect, shallowly galeate, narrowly obovate to narrowly oblong, acute, rarely obtuse, 10–15 mm long and 3–6 mm wide; spur usually upcurved, rarely straight, tapering towards the apex, (7.5)–10–13 mm long and 1–2 mm in diameter. *Lateral sepals* narrowly oblong, sub-oblique, acute, spreading, 10–14 mm long and 2.5–5 mm wide. *Petals* lorate, zygomorphic, 7–8 mm long, basal anticous lobe reduced to a fold, apex usually unequally bifid, acute. *Lip* 10–17 mm long, apical tooth pendant, filiform, 4–8 mm long, mesochile flat, 3–4 mm wide. *Column* short, rostellum lateral lobes horn-like, central lobe reduced to a small fleshy blob.

NOMENCLATURE AND TYPIFICATION

Schizodium bifidum (Thunb.) Reichb. f. in *Flora* 66: 460 (1883); Dur. & Schinz in *Consp. Fl. Afr.* 5: 113 (1892); Kraenzl. in *Orch. Gen. Sp.* 1: 729 (1900); Schltr. in *Bot. Jahrb.* 31: 302 (1901), excl. var. and syn. *S. obtusatum* Lindl. and *S. longipetalum* Lindl.

Satyrium bifidum Thunb. in *Prod. Fl. Cap.*: 5 (1794). Type: Herb. Thunberg 21430 (UPS!, holotype).

Disa bifida (Thunb.) Sw. in *Kongl. Vet. Acad. Handl.*: 212 (1800); Thunb. in *Fl. Cap.*: 58 (1807); H. Bol. in *Trans. S. Afr. phil. Soc.* 5: 163 (1888), *J. Linn. Soc.* 25: 201 (1889).

Schizodium rigidum Lindl. in *Gen. Sp. Orch.*: 360 (1838). Type: Swellendam, Buffelsjag River, Hills at Sparbos. *Drège 1231e* (K!, holotype); Schltr. in *Bot. Jahrb.* 31: 303 (1901); Rolfe in *Fl. Cap.* 5. 3: 255 (1913).

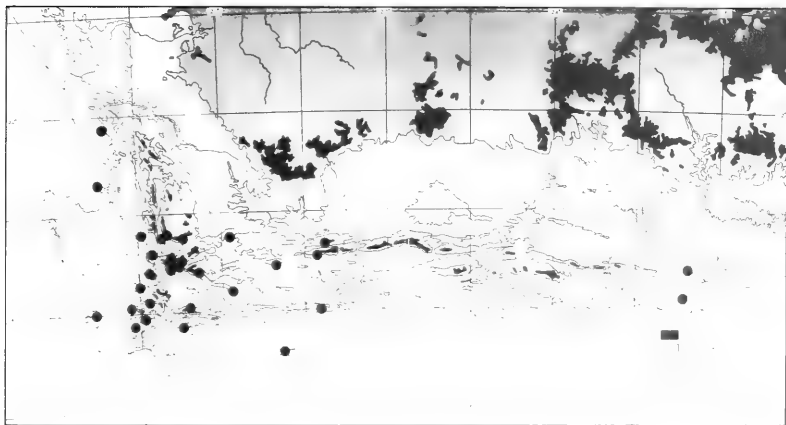


FIG. 4.
Distribution of *S. bifidum*.

Icon: H. Bolus, *Icones Orch. Austro-Afr.* 2: tt 94, 95 (1911).

This species has caused little confusion. Lindley was probably not aware of the nature of the Thunberg's *Disa bifida*, and it was left to Reichenbach to recognize its affinities when he had the opportunity in 1865 to study Thunberg's herbarium. Rolfe (1913) upheld the name *S. rigidum* in preference to the older *S. bifidum* because of the "Kew Rule" then applied by English botanists.

Schlechter (1901) appears to have misapplied the concept of *S. bifidum*, as the synonyms that he cites under this name are allied to the *S. obliquum* group, and he maintains *S. rigidum* as a distinct entity.

TAXONOMY, ECOLOGY AND DISTRIBUTION

Schizodium bifidum is closely allied to *S. inflexum*. The vast majority of collections can readily be distinguished by the larger flowers, the broader dorsal sepal, and the slender, tapering, ascending spur of *S. bifidum*. However, several populations in the Ceres and Bainskloof areas appear to be somewhat intermediate. As these populations occur in the ecological overlap zone of the two species, they could well be the results of ancient hybridization.

S. bifidum occurs throughout the fynbos region, except for a large gap between the Gouritz River and Port Elizabeth (Fig. 4). Populations are almost always restricted to fairly flat areas of deep sand. The species also tends to occur at relatively low altitudes, except at the inland localities. Recorded precipitation over the distribution area ranges from about 500 mm p.a. to over 1 000 mm p.a. Rainfall distribution also ranges from a clear winter-rainfall regime in the west,

to a spring maximum rainfall (but with precipitation throughout the year) in Port Elizabeth.

Flowering in this species occurs in September and October, with occasional specimens in flower collected as early as July. Flowering time is closely linked to altitude, and populations from the Worcester and Ceres mountains flower last.

REPRESENTATIVE COLLECTIONS

Ceres, Skurfteberg Pass into the Agterwitsenberg Valley, Sept., *Linder* 575 (BOL); Ladismith, south slopes of the Swartberg below Toverkop, c. 1 000 m, Aug., *Esterhuysen* 333896 (BOL); Somerset West, moist sand near Sir Lowry's Pass, 150 m, July, *Schlechter* 1175 (BOL).

3. *Schizodium inflexum* Lindl.

Petals without a basal anticus lobe; sepals 7–12 mm long and 2–3.5 mm wide; spur base in line with the base of the dorsal sepal, generally straight or curved down, base usually swollen.

Plants straight or subflexuose, 80–350 mm tall, wiry, nitid, pale green to purple. *Leaves* basal and cauline, basal leaves spreading, petiolate, the blade oblanceolate to narrowly oblanceolate, apiculate, 10–20 mm long and 5–9 mm wide, the margins occasionally undulate, the blade often with two lines of dark spots on the upper surface and purple below; cauline leaves more or less closely sheathing the stem, distant, acute to acuminate, 6–16 mm long. *Inflorescence* 1–7 flowered; bracts similar to the cauline leaves; pedicel rarely exserted from the bracts, 2–7 mm long, ovary 3–10 mm long; flowers pink, sepals with darker spots on the back along the midrib, tooth of lip usually dark purple, mesochile of lip with darker spots along the margin, petal apex darker. *Dorsal sepal* erect, galeate, obtuse to acute, narrowly oblong, 6–8 mm long and 2–4 mm wide; spur more or less straight, rarely somewhat upcurved or decurved, upper and lower margins usually parallel, apically rounded or emarginate, the base often widened, 5–8 mm long and 2–4 mm deep. *Lateral sepals* narrowly oblong, obtuse to acute, sub-oblique, spreading, 7.5–10–(12) mm long and 2–3–(4) mm wide. *Petals* lorate, zygomorphic, apically acute, truncate or shallowly bifid, 5–7 mm long, basal anticus lobe reduced to a fold. *Lip* 9–13–(16) mm long, apical tooth pendant, filiform, 3–7 mm long, mesochile margins flat or undulate, 3–5 mm wide. *Column* short, rostellum lateral lobes horn-like, central lobe very reduced.

NOMENCLATURE AND TYPIFICATION

Schizodium inflexum Lindl. in Gen. Sp. Orch.: 360 (1838). Type: Cape Province, *Burchell* (K!, holotype); Dur. & Schinz in Consp. Fl. Afr. 5: 113 (1892); Kraenzl. in Orch. Gen. Sp. 1: 727 (1900); Schltr. in Bot. Jahrb. 31: 304 (1901); Rolfe in Fl. Cap. 5.3.: 254 (1913).

Disa inflexa Mund. Lindl. in Gen. Sp. Orch.: 360 (1838), nom. nud.; Bolus in Trans. S. Afr. phil. Soc. **5**: 162 (1888), J. Linn. Soc. **25**: 201 (1889).

Icones: H. Bolus, Icones Orch. Austro-Afr. **2**:t. 93 (1911). Kidd, Wild Flowers of the Cape Peninsula, Pl. 94.7 (1950). Schelpe, An introduction to the South African orchids, Pl. 53 (1966).

TAXONOMY, ECOLOGY AND DISTRIBUTION

The relationship to *S. bifidum* is discussed above.

S. inflexum can, by its distribution, be described as being ubiquitous in the Cape Flora (Weimarck, 1941). It occurs along the fold mountains from Nieuwoudtville to Humansdorp, and inland it extends to the Witteberg and the Elandsberg. It has been collected on every major mountain range in the Cape Floral Area.

It is essentially a mountain species, with no collections from below 300 m, and the majority of collections are from between 900 and 1 200 m. It is usually associated with shallow soils overlying Table Mountain Sandstone bedrock, or with areas which are very rocky. In this habitat it occurs both in well-drained habitats, or in slight seepages, often associated with *Restio curviramis* (especially in the Cedarberg and the Bokkeveld mountains).

The climate in this habitat is severe, with snow in the winter months. No reliable rainfall data are available for most of the localities, but it is probably in excess of 1 000 mm p.a.

Flowering occurs mainly in October and November, but occasional collections have been made in September (especially at the western end of the distribution), and in December and even January. Vogel (1959) discussed the possible pollination mechanism of this species, and concluded that it is best adapted for pollination by hymenopterans. This work has not been substantiated by field observations.

REPRESENTATIVE COLLECTIONS

Uniondale, Joubertina, north slope of the Tsitsikamma mountains, in a swamp, Nov., *Esterhuysen 10633* (BOL); Ceres, shale band from Witelskloof to Buffelshoek Peak, 1 200 m, Oct., *Esterhuysen 26352* (BOL).

4. *Schizodium obliquum* Lindl.

Petals with large anticus lobes; spur constricted at the base; lateral sepals 5–14 mm long.

Plants 55–290 mm tall, stem strongly flexuose, wiry, nitid, pale green to purple. *Leaves* basal and cauline; basal leaves petiolate, blade broadly obovate to

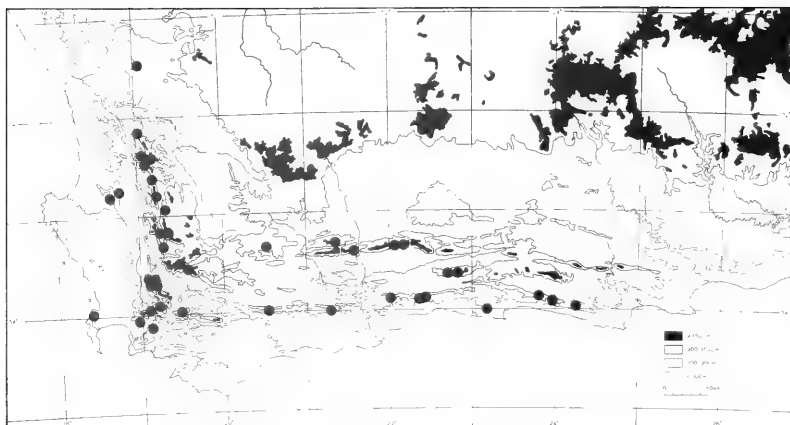


FIG. 5.
Distribution of *S. inflexum*.

spathulate, apiculate, 5–14 mm long and 3–9 mm wide; cauline leaves lanceolate, acuminate, 7–18 mm long, the upper $\frac{2}{3}$ free and distant from the scape. *Inflorescence* (2)–6–(9) flowered; bracts similar to the cauline leaves; pedicels 3–18 mm long, well exerted from the bracts, ovaries 2–10 mm long; flowers pale pink, lip with a dotted pattern. *Dorsal sepal* sub-erect, usually forming a 45° angle with the lateral sepals, lanceolate, sub-obtuse to sub-acuminate, 5–10 mm long and 1.5–4 mm wide; spur linear to clavate, 3–9 mm long, obtuse to slightly bifid, straight or somewhat bent up or down, dorsoventrally constricted at the base. *Lateral sepals* lanceolate obtuse to acuminate, usually acute, 5–14 mm long and 1.5–4 mm wide. *Petals* apex variously bifid, occasionally the anterior lobe much larger than the posterior lobe, basal anticus lobe large, the margins usually serrate, petals included in the galea. *Lip* pandurate; apical tooth terete, wedge-shaped to subulate, (1)–2–(5) mm long, darkly coloured; mesochile 1.5–5 mm wide, margins smooth or slightly crenate; hypochile concave, pale. *Column* short, anther reflexed, rostellum short, erect, stigma pulvinate.

TAXONOMIC NOTES

Lindley (1838) divided this group into three taxa. He differentiated them on petal, lip, sepal and spur shape. Lindley only had one specimen available for each of his taxa, and as a result most of the differentiating characters can now be shown to be variable, even within one population. Rolfe (1913) maintained Lindley's three species, but differentiated them on size (*S. obliquum*) and spur shape (*S. obtusatum* and *S. clavigerum*). This approach is more realistic.

A detailed analysis of 45 collections (including three population samples) showed that the material from the Cape Peninsula, Cape Hangklip, the flats eastwards to Stellenbosch and northwards to Darling, can be separated from the remaining collections. The most obvious differentiating characters are flower size and plant size (Fig. 6), in which there is partial separation. On the Peninsula, the lateral sepals tend to be, relative to the dorsal sepal, longer than in the rest of the distribution area. Spur shape also shows less variation on the Peninsula than it does elsewhere. It is usually dorsoventrally flattened, narrowly cuneiform and straight. The only geographic area of overlap is at Stellenbosch. *Strey 530* contains elements that could be referred to both subspecies. *Farnham* (Sept. 1885, Stellenbosch) falls clearly in the variation range of the Peninsula subspecies.

Among the remaining collections there is some variation in the dorsal sepal/lateral sepal length ratios, and in spur shape. But both these characters do not relate simply to the distribution patterns, and do not appear to be related to each other. In general, populations from Sir Lowry's Pass eastwards tend to have slender to cuneate spurs, and populations inland of the Du Toits Kloof and Bainskloof mountains often have very clavate spurs (e.g. *Linder 1120*).

Although there might be a link between the spur morphotype and the habitat of the population, with the more clavate forms occurring in wet sandy flats and the slender spurred forms occurring on well-drained mountain slopes, there are as yet insufficient data to demonstrate this link.

4a. *Schizodium obliquum* Lindl. ssp. *obliquum*

Lateral sepals generally longer than 8.5 mm, about $\frac{1}{3}$ longer than the dorsal sepal; plants 100–150–250 mm tall; from the Cape Peninsula and the Cape Flats to Darling.

NOMENCLATURE AND TYPIFICATION

Schizodium obliquum Lindl. in Gen. Sp. Orch.: 359 (1838). Type: Cape of Good Hope, *Forbes* (K!, holotype); Dur. and Schinz in Consp. Fl. Afr. 5: 114 (1892), excluding syn.; Kraenzl. in Orch. Gen. Sp. 1: 728 (1900); Rolfe in Fl. Cap. 5.3: 256 (1913).

Disa obliqua (Lindl.) H. Bol. in Trans. S. Afr. phil. Soc. 5: 162 (1888); in J. Linn. Soc. 25: 201 (1889), excl. syn.

Icones: H. Bolus, Icones Orch. Austro-Afr. 2. t.96 (1911). Kidd, Wild Flowers of the Cape Peninsula, Pl. 49.1 (1950).

Lindley (1838) described three species, here considered as synonyms (*S. obtusatum*, *S. obliquum* and *S. clavigerum*), in the same publication. All three names are valid, and none have priority. As *S. obliquum* has been used most often, this name is upheld here.

Schlechter (1901) ignored the name *S. obliquum*, and included the other synonyms and specimens referable to this species in his *S. bifidum*. Bolus (1911) followed this treatment.

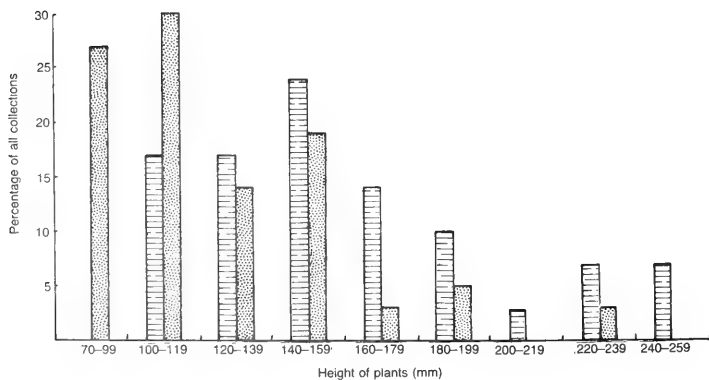
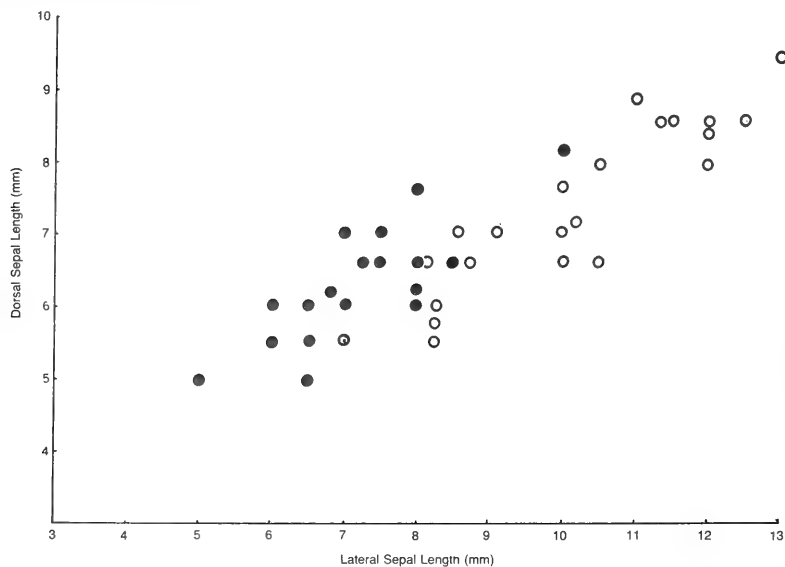
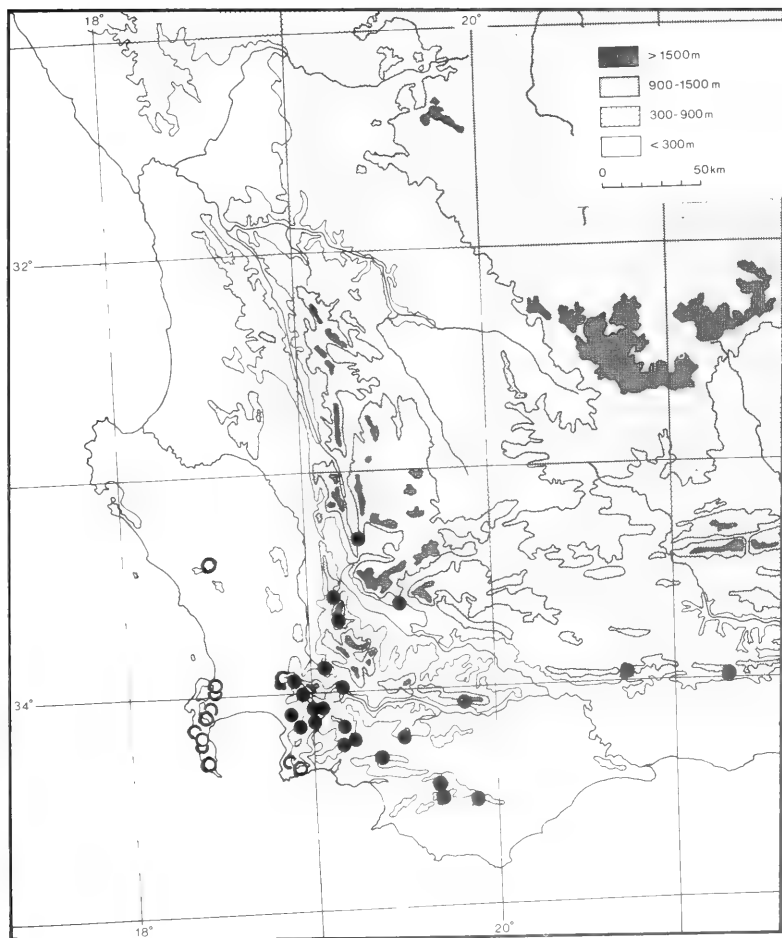


FIG. 6.

Variation in *S. obliquum*. The solid circles and right-hand (dotted) columns represent *ssp. clavigerum*, and the open circles and left-hand (horizontally barred) columns represent *ssp. obliquum*.



G.P. 5 (4).

FIG. 7.

Distribution of *S. obliquum*. Open circles represent the ssp. *obliquum* and solid circles represent the ssp. *clavigerum*.

ECOLOGY AND DISTRIBUTION

This subspecies occurs in the Cape Peninsula, with outlier populations at Darling and at Stellenbosch.

Populations studied all occurred on deep sand, rarely in the vicinity of rock outcrops. The sand may be of Recent origin or derived from Table Mountain Sandstone. In general the sand is damp in winter and spring, in the Darling population it is seasonally wet, with scattered subpopulations occurring on the margins of seasonal pools. Precipitation in the area ranges from near 500 mm p.a. at Darling to over 1 000 mm p.a. at Claremont, Cape Peninsula (W.B. 29). Rainfall occurs predominantly in the winter.

Flowering occurs mainly in August and September, occasionally in July and October. The altitude range of the species is from sea-level to c. 300 m.

REPRESENTATIVE COLLECTIONS

Cape Peninsula, Muizenberg mountain, 300 m, July, *Bolus 7037* (BOL); Malmesbury, Mamre Rd., Riverlands, August, *Linder 1125* (BOL, K, PRE).

4b. *Schizodium obliquum* Lindl. subsp. *clavigerum* (Lindl.) Linder

Lateral sepals generally shorter than 8,5 mm, about as long as the dorsal sepal; plants 80–120–240 mm tall, from the Western Cape excluding the Cape Peninsula and the Flats stretching to Darling.

NOMENCLATURE AND TYPIFICATION

Schizodium obliquum Lindl. ssp. *clavigerum* (Lindl.) Linder, stat. nov. et comb. nov.; basionym: *Schizodium clavigerum* Lindl. in Gen. Sp. Orch.: 360 (1838). Type: Western Cape, between Paarl and Groenekloof, *Drège 1231d* (K!, holotype; P!, S!); Dur. & Schinz in Consp. Fl. Afr. 5: 113 (1892); Kraenzl. in Orch. Gen. Sp. 1: 727 (1900); Rolfe in Fl. Cap. 5.3: 257 (1913).

Disa clavigera (Lindl.) H. Bol. in Trans. S. Afr. phil. Soc. 5: 163 (1888); in J. Linn. Soc. 25: 201 (1889).

Schizodium obtusatum Lindl. in Gen. Sp. Orch.: 359 (1838). Type: Paarl, Du Toits Kloof, *Drège 1231cc* (K!, holotype; G!, P!); Kraenzl. in Orch. Gen. Sp. 1: 729 (1900); Rolfe in Fl. Cap. 5.3: 256 (1913).

Schizodium gueinzii Reichb. f. in Linnaea 20: 694 (1847). Type: *Gueinzius s.n.* (W!, iconotype); Dur. & Schinz in Consp. Fl. Afr. 5: 113 (1892); Kraenzl. in Orch. Gen. Sp. 1: 730 (1900).

Disa gueinzii (Reichb. f.) H. Bol. in J. Linn. Soc. 25: 201 (1889).

Schizodium bifidum (Thunb.) Reichb. f. var. *clavigerum* (Lindl.) Schltr. in Bot. Jahrb. 31: 303 (1901).

Schizodium modestum L. Bol. in Fl. Pl. S. Afr. 19 Pl. 752 (1939). Type: Stellenbosch, near Somerset West, *Prentice 13900* (BOL!, holotype).

Icon: Fl. Pl. S. Afr. 19, Pl. 752 (1939).

Of the two names available for this subspecies, *S. clavigerum* was selected because it had already been applied at the infraspecific level, and is also better known than *S. obtusatum*.

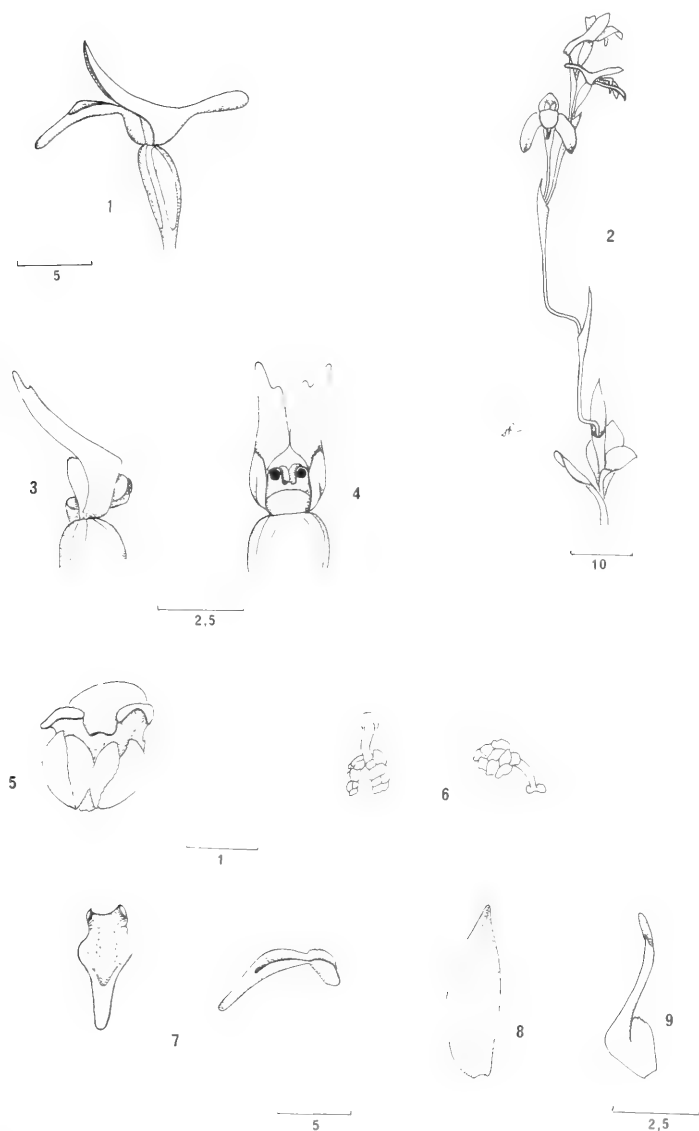


FIG. 8.

S. obliquum Lindl. ssp. *clavigerum* (Lindl.) Linder. From *Linder*. 1. Flower without lateral sepals, 2. Plant, 3 & 4. Petals & rostellum, 5. Rostellum rear view, 6. Pollinaria, 7. Lip in 3 dimensions, 8. Lateral sepal, 9. Lip.

No type specimen could be found for *S. guenzii*. In the Reichenbach herbarium in Vienna a drawing of the type exists; this is assumed to be an iconotype. The type locality of the species is unknown.

Schlechter (1901) included almost the whole of the species in *S. bifidum*, but separated out *S. clavigerum* at varietal level. He does not refer to *S. gueinzii* at all. Kraenzlin (1900) includes *S. gueinzii* under his "species dubiae".

S. modestum cannot be separated from the remainder of this subspecies, and the differential characters mentioned by Bolus are not valid.

ECOLOGY AND DISTRIBUTION

This subspecies extends from Bredasdorp in the east to Ceres in the west (Fig. 7), but does not occur on the Flats between the Cape Peninsula and Darling.

Habitat notes for collections from the eastern part of the distribution range all indicate stony sandy conditions on hills or mountain slopes, i.e. a well-drained habitat. Some of the records indicate that the area was burnt recently. Field studies on the population on the summit of Sir Lowry's Pass (*Linder* 577) supported these observations. The population was extensive, and occurred on well-drained Table Mountain Sandstone derived sand, with numerous stones in it. The area had been burnt some two years before that. The clavate form from Wolseley (*Linder* 1120) occurred in seasonally wet sand, in the valley floor. The population was subdivided into numerous subpopulations scattered along the margins of the seasonal ponds. There is, however, a lack of detailed habitat information about this species.

Rainfall over the distribution range varies from about 600 mm p.a. (over most of the range) to over 1 000 mm p.a. in the Jonkershoek to Paarl area. The rainfall is concentrated in the winter. This subspecies probably never experiences snow in the winter months.

Flowering occurs mostly in September, but specimens have been collected in flower from June to November.

REPRESENTATIVE COLLECTIONS

Tulbagh, Romansriver Railway Station, in seasonally wet sand, Aug., *Linder* 1120 (BOL, PRE); Caledon, Steenbras River, Oct., *Schlechter* 5386 (PRE).

5. *Schizodium cornutum* (L.) Schlechter

Lateral sepals usually longer than the dorsal sepal, recurved, acuminate, 12–18 mm long, with a wide base; dorsal sepal narrow acuminate.

Plant flexuose, wiry, nitid, 80–300 mm tall. *Leaves* basal and cauline; basal leaves petiolate, spatulate, apiculate, 6–16 mm long and 3–7 mm wide; cauline leaves 1–4, lanceolate, acute to acuminate, 6–18 mm long, the upper half free

and distant from the scape. *Inflorescence* 1–6 flowered; bracts like cauline sheaths; pedicels 4–15 mm long, mostly well exerted from the bracts, usually twice as long as the bracts, ovaries 3–10 mm long; flowers white to rarely rose-red, the lip pale green. *Dorsal sepal* linear, acuminate, recurved, convex, the basal part forming a hood over the petals, 7–12 mm long and 1.5–2 mm wide; spur 5–10 mm long, straight or slightly decurved, bifid. *Lateral sepals* linear-lanceolate, usually widest at the base, acuminate, recurved, 12–18 mm long. *Petals* 3–5 mm long, apex evenly to unevenly bifid, anticus lobe reduced to a fold. *Lip* tripartite, pandurate: apical tooth (2)–8–(13) mm long, subulate, pendant; mesochile margin often undulate; hypochile small. *Column* short, anther reflexed, rostellum short and broad.

NOMENCLATURE AND TYPIFICATION

Schizodium cornutum (L.) Schltr. in Ann. Trans. Mus. **10**: 248 (1924).

Satyrium cornutum L. in Pl. Rar. Afr.: 27 (1760). Type: Herb. Burman (G!, holotype).

Orchis biflora L. in Sp. Pl. ed. 3: 1330 (1764). Type: As for *Satyrium cornutum* L.

Schizodium biflorum (L.) Dur. & Schinz in Consp. Fl. Afr. **5**: 113 (1892); Kraenzl. in Orch. Gen. Sp. **1**: 725 (1900); Schltr. in Bot. Jahrb. **31**: 301 (1901).

Satyrium tortum Thunb. in Prod. Pl. Cap.: 5 (1794). Type: Thunb. herb. 21465 (UPS!, holotype).

Disa torta (Thunb.) Sw. in Kongl. Vet. Acad. Handl. **31**: 211 (1800); Thunb. in Fl. Cap.: 61 (1807); H. Bol. in Trans. S. Afr. phil. Soc. **5**: 161 (1883); in J. Linn. Soc. **25**: 201 (1889).

Schizodium arcuatum Lindl. in Gen. Sp. Orch.: 359 (1838). Type: Near Caledon, Drège 1231g (K!, holotype; G!); Rolfe in Fl. Cap. **5.3**: 257 (1913).

Orchis satyroides biflora bulbo indiviso, corolla galea unicalcarata, labello indiviso apice lanceolata L. in Amoen. Acad. **6**: 109 (1763).

Icon: H. Bolus, Icones Orch. Autro-Afr. **1**: t.33 (1893).

Satyrium cornutum L. was described from a specimen in the Burman herbarium, which is now in Geneva. The sheet of *S. cornutum* is in a bad condition, and the specimen not well pressed. However, the narrow reflexed lateral sepals and the long tooth of the lip indicate the taxon to which the name applies (see Figure 9).

In 1763 Linnaeus transferred *Satyrium cornutum* to the genus *Orchis*, but did not indicate a new specific epithet. He diagnosed the taxon merely as “*Orchis satyroides biflora*”, followed by the same diagnosis. This name has to be regarded as a polynomial. A year later he published the taxon under the name

Orchis biflora. This is therefore a later name for the epithet "*cornutum*". Thunberg did not seem to be aware of the correct nature of the Linnaean *Satyrium cornutum*, when he published his *Satyrium tortum*. Lindley, in turn, did not refer to either the Linnaean nor the Thunberg names. The confusion was resolved by Durand and Schinz (1892) and they were unaware of the earlier *Satyrium cornutum* of Linnaeus, and called the taxon *S. biflorum*. Schlechter (1924) finally made the correct combination for the species.

DISTRIBUTION AND ECOLOGY

The distribution of this species is indicated in Figure 11. This falls in the Western Group of Weimarck (1941).

Most of the localities are found below 900 m, although on the drier edges of the distribution range some populations occur at 1500 m. Populations usually

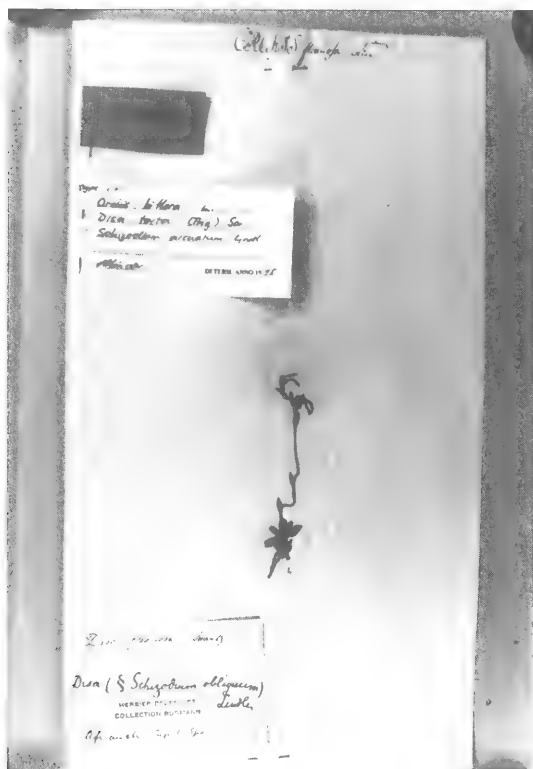


FIG. 9.1.

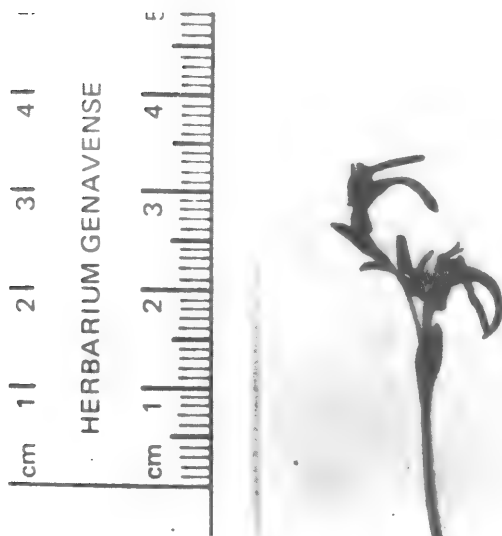


FIG. 9.2.

Holotype of *S. cornutum* (G). 1. The whole sheet. 2. Inflorescence.

occur in alluvial or flat sandy areas, usually on sand derived from Table Mountain Sandstone. Rainfall over the distribution range varies from about 400 mm p.a. at Nieuwoudtville to over 700 mm p.a. at Stellenbosch (W.B. 29), and of this about 70 % falls between May and September (inclusive) (W.B. 35). Flowering occurs between August and September, with occasional collections from as early as July, and some higher altitude collections from as late as October.

REPRESENTATIVE COLLECTIONS

Calvinia, 3 miles west of Nieuwoudtville, Aug., *Lewis 2337* (SAM); Ceres, Gydouw Pass, Aug. 1939, *Leipoldt* (BOL); Clanwilliam, Olifants River, 35 Aug. 1894, *Schlechter 5012* (BOL).

6. *Schizodium longipetalum* Lindl.

Anterior petal lobes at least as long as the limb of the petal, filiform, reflexed, similar to the tooth of the lip; leaves crisped, undulate.

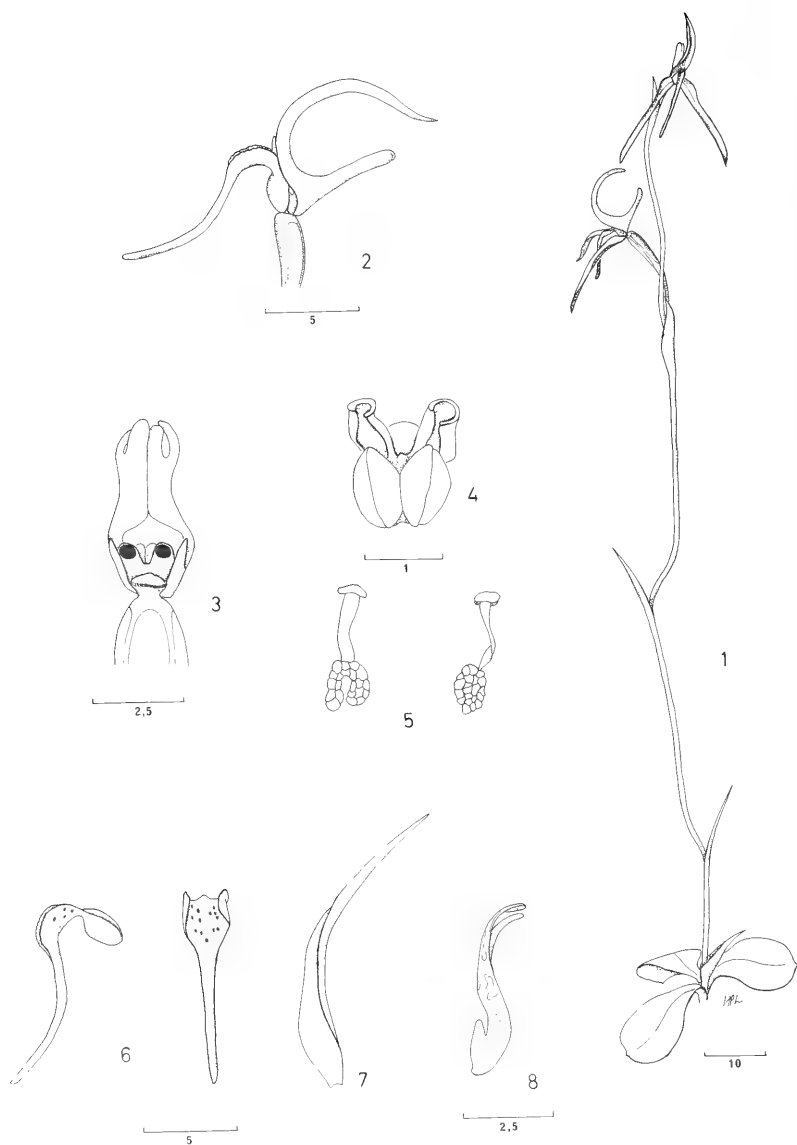
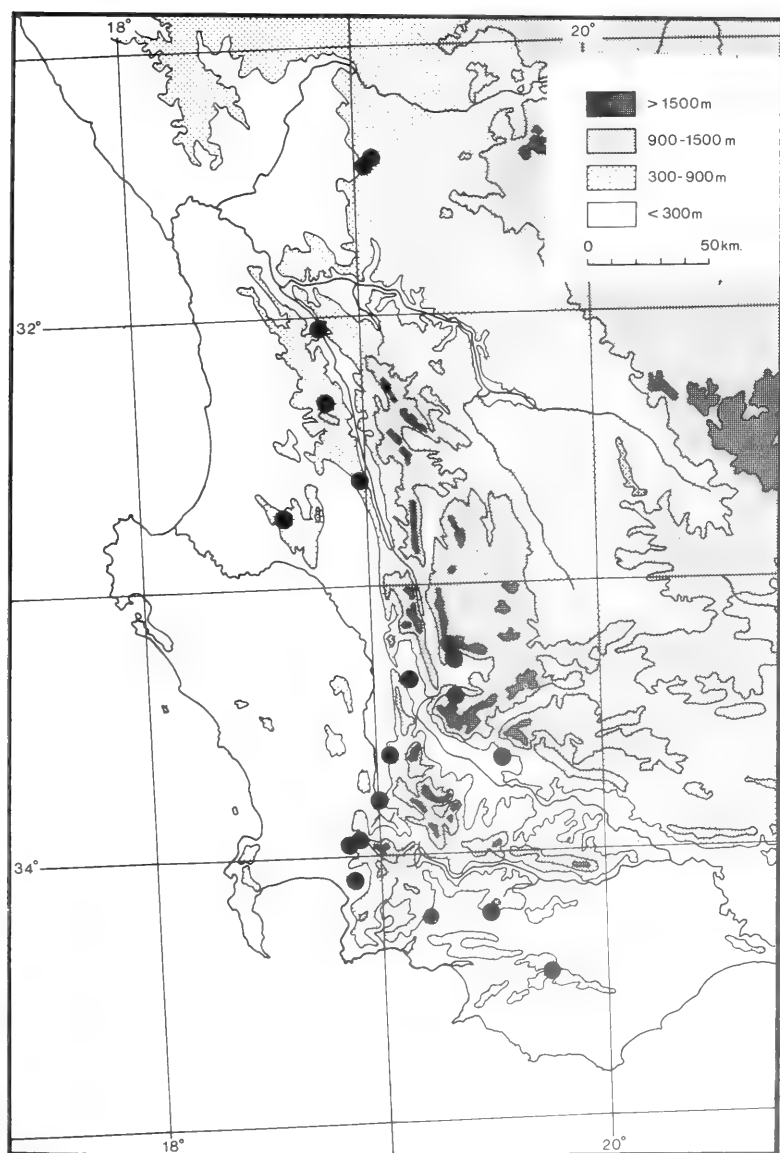


FIG. 10.

S. cornutum (from Linder). 1. Whole plant, 2. Flower with the lateral sepals removed, 3. Front view of petals and column, 4. Rear view of rostellum, 5. Pollinaria, 6. Lip in 3 dimensions, 7. Lateral sepal, 8. Petal.



G.P.-S. (L).

FIG. 11.
Distribution of *S. cornutum*.

Plant 7–20 mm tall, scape wiry, flexuose. *Leaves* basal and cauline; basal leaves petiolate, spatulate, lorate, apiculate, 8–12 mm long and 3–6 mm wide, margins crisped-undulate; cauline leaves 2–3, oblong lanceolate, acute to acuminate, 8–13 mm long, the upper half free. *Inflorescence* (2)–6–(7) flowered; bracts similar to the cauline leaves; pedicels 3–10 mm long and ovaries 3–5 mm long; flowers greenish-yellow, lip mesochile and base of the lateral sepals with purplish spots, filiform processes of the petals and lip dull purple. *Dorsal sepal* recurved, lanceolate, acute to very acuminate, 7–12 mm long and 2–3 mm wide; spur 2–3 mm long, bluntly bifid, straight to slightly decurved, constricted at the base. *Lateral sepals* narrowly lanceolate, acuminate to very acuminate, recurved, 8–12 mm long and 1.5–2 mm wide. *Petals* bent near the base, zygomorphic, 2–3 mm long, basal anticous lobe absent, apex unequally bifid with the anterior tooth filiform, reflexed, at least twice as long as the petal limb, the posterior tooth very small or absent. *Lip* pandurate, the hypochile and the epichile sub-equal, 1.3–3 mm wide, the apical tooth subulate, 3.5–9–12 mm long, often reflexed. *Column* short, anthers reflexed, rostellum tridentate, stigma pulvinate.

NOMENCLATURE AND TYPIFICATION

Schizodium longipetalum Lindl. in Gen. Sp. Orch.: 359 (1838). Type: Paarl, Paarlberg between 1 000 and 2 000 feet, *Drège* 8273 (K!, holotype; P!, S!); Dur. & Schinz in Consp. Fl. Afr. 5: 115 (1892); Kraenzl. in Orch. Gen. Sp. 1: 725 (1900); Rolfe in Fl. Cap. 5.3: 258 (1913).

Disa longipetala (Lindl.) H. Bol. in J. Linn. Soc. 25: 201 (1889).

Schizodium antenniferum Schltr. in Bot. Jahrb. 24: 426 (1898). Type: Piketberg, *Schlechter* 5248 (B, holotype; BOL!, PRE!, SAM!, Z!); Schltr. in Bot. Jahrb. 31: 305 (1901).

Schizodium bifidum sensu Schlechter, partly, non Reichb. f., in Bot. Jahrb. 31: 303 (1901).

Icon: H. Bolus, Icones Orch. Austro-Afr. 1: t.88 (1896).

This quite distinct species is clearly described and typified. However, the material from the Piketberg, on which Schlechter based his *S. antenniferum*, is somewhat different, though not enough to warrant specific distinction. Schlechter (1901) also included Lindley's *S. longipetalum* in his large variable *S. bifidum*. The illustration in Bolus (1896) was probably done from the type collection of *S. antenniferum*.

TAXONOMY, DISTRIBUTION AND ECOLOGY

S. longipetalum is only known from four localities, two of which might be extinct. It appears as if the species is restricted to proteoid shrubland on gravelly soils derived from Table Mountain Sandstone, in a rainfall regime of c. 700 mm p.a., of which most falls in winter (W.B. 35). Populations appear to be scattered, and are difficult to find in the dense vegetation.

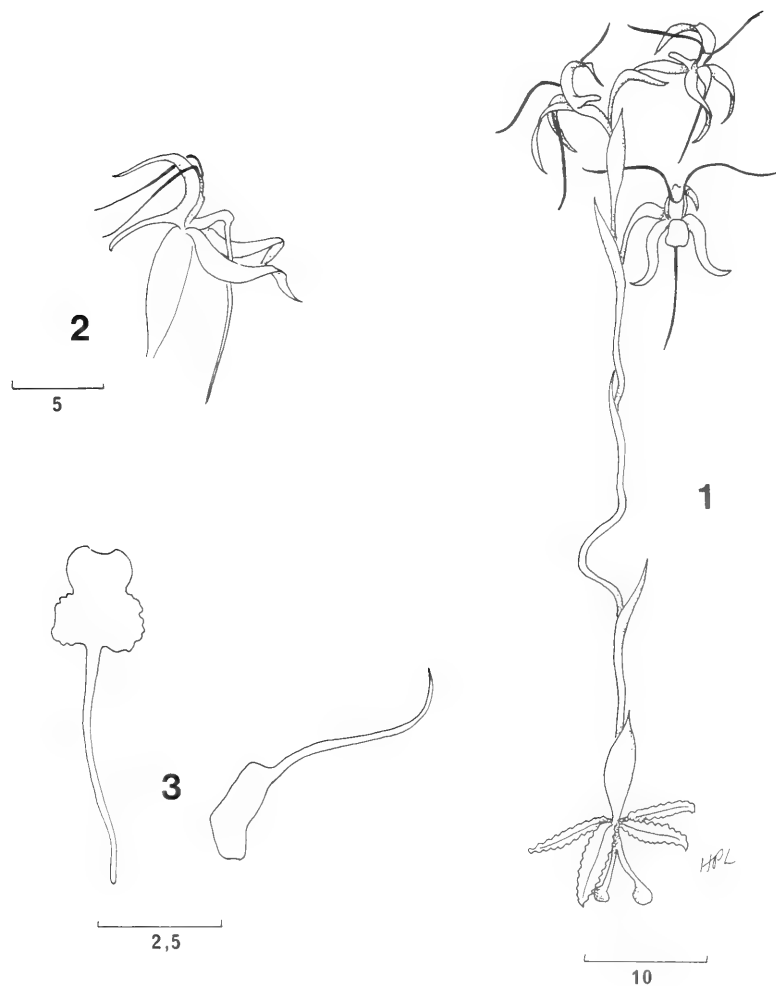
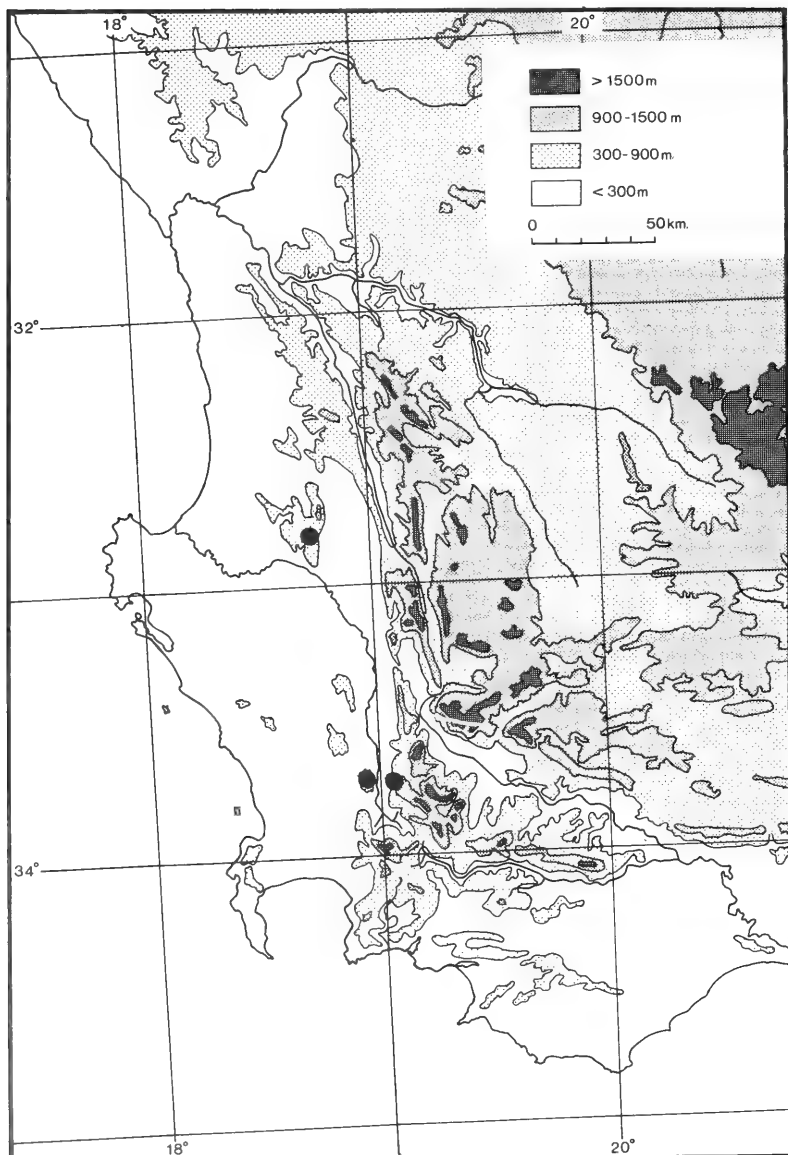


FIG. 12.
S. longipetalum (adapted from Bolus 1896). 1. Whole plant, 2. Detail of flower, 3. Petal and lip in 2 dimensions.



G.P.-S. (L).

FIG. 13.
Distribution of *S. longipetalum*.

The material from the Worcester and Paarl areas is fairly uniform, and falls well within the concept of *S. longipetalum*. However, the material known from the Piketberg has longer anterior petal lobes and a longer lip tooth. On this material Schlechter based his *S. antenniferum*. The population is also isolated from the rest of the species, and could be regarded as a geographical form of that species. However, not enough information is available about the Piketberg population which last flowered in 1971, and it is at this stage best included in *S. longipetalum*.

REPRESENTATIVE COLLECTIONS

Paarl District, 5 m south of Huguenot, Aug., *Salter 4732* (BOL).

SPECIES EXCLUDED

Schizodium maculatum (L.f.) Lindl. in Gen. Sp. Orch.: 360 (1838).

This is *Disa maculata* L.f., as in H. Bol. in J. Linn. Soc. 20: 478 (1884).

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Names not recognised are printed in italics.

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APPENDIX 1. LIST OF SPECIMENS STUDIED.

The specimens are listed alphabetically according to the name of the collector. The figures in brackets refer to the number of the taxon in the text. Herbaria from which each collection has been studied are indicated by the letter codes of Holmgren and Keuken (1974).

Ackerman in STE 17026 (4b) STE—Acocks 1946 (2) S; 2170 (1) S; 2406 (4b) S; 2436 (2) S; 2451 (2) S; 2512 (5) S; 15509 (1) PRE. K; 19724 (5) PRE; 21409 (2) PRE; 22489 (2) PRE; 23737 (2) PRE; 24038 (2) PRE—Adamson in SAM 39048 (1) SAM—Alexander (4a) PRE—Anderson in STE 29988 (1) PRE. STE—Andrag in STE 8569 (2) STE—Andreae 672 (3) PRE. STE; 1208 (3) PRE; 1304 (3) BOL. STE.

Bachman 1632 (5) Z; 1633 (1) Z; 1972 (5) Z—Baker 264 (4b) NBG, SAM—Barker 3096 (1) NBG; 3109 (2) NBG; 3122 (1) NBG; 3127 (3) NBG; 3809 (4b) SAM; 4129 (1) NBG; 4786 (5) NBG; 7495 (2) NBG; 10634 (2) NBG—Barnard in SAM 28947 (3) SAM—Basson (5) STE—Bodkin 7019 (2) BOL. K; (3) BOL—Bolus 3550 (3) BOL; 3742 (4a) BOL. K. PRE; 3882 (3) BM, BR. K. Z; 4332 (1) BM. BOL. K. Z; 5444 (5) K; 5445 (5) BOL. K; 5446 (4b) BOL; 5923 (4b) BOL; 7037 (4a) BOL; 7481 (2) BOL; 7514 (4b) BOL; 11647 (3) BR. BOL; 13900 (4b) BOL; 19579 (5) BOL; 19580 (3) BOL; 23369 (3) BOL; (2) BOL; (3) BOL; (3) BOL; (4b) BOL—Bond 580 (3) NBG; 639 (3) NBG; 649 (1) NBG—Booyesen 67 (3) NBG—Boucher 429 (4b) STE; 1370 (4a) STE; 2879 (1) STE—Bowie 6 (4b) BM; 412 (4a) G—Brenan 14032a (3) K—Burbury 272 (4a) BM—Burchell 655 (3) K; 7107 (3) K.

Commerson (1) G—Compton 3383 (2) BOL; 4148 (1) BOL; 5677 (4b) NBG, SAM; 10080 (3) NBG; 11948 (2) NBG; 11979 (2) NBG; 13293 (4a) NBG, SAM; 13473 (4b) NBG, SAM; 13482 (4b) NBG, SAM; 13828 (4b) NBG, SAM; 13994 (3) NBG; 15743 (4a) NBG, SAM; 18334 (1) NBG; 18798 (3) NBG; 19919 (2) NBG; 20115 (2) NBG; 20179 (4a) NBG, SAM; 20999 (2) NBG; 21813 (3) NBG—Cummings 4 (2) GRA; 263 (2) GRA; (5) BOL.

Davis in SAM 49376 (3) SAM—Davis & Stokoe in SAM 22018 (4b) SAM; in SAM 61031 (4b) PRE; in SAM 61036 (1) PRE, SAM—De Villiers in STE 8557 (1) STE; (5) STE—Drège 56 (2) GRA, PRE, SAM; (2) BOL. Z—Drège 1231a (3) P; 1231b (5) G, K, P; 1231c (4b) K, P; 1231cc (3) P; 1231f (3) P; 1231g (5) P; 1238 (1) G, K, P, S—Duemmer 553a (3) BM—Du Plessis (1) STE.

Ebersohn 269 (4b) NBG, SAM—Ecklon 321 (1) Z—Ecklon & Zeyher 63 (1) SAM; 64 (5) K, PRE, Z; (3) S—Edwards in BOL 13901 (5) BOL. Z; (4b) G—Esterhuysen 3117 (3) BOL. PRE; 3119 (3) BOL; 3180 (2) BOL; 6443 (3) BOL; 6793 (3) BOL. PRE; 8209 (2) BOL; 9250 (3) BOL; 9445 (3) BOL; 10633 (3) BOL; 12151 (3) BOL. PRE; 13981 (2) BOL; 14077 (2) BOL; 15912 (2) BOL. PRE; 16388 (3) BOL. PRE; 17444 (1) BOL. M; 20355 (5) BOL; 20357 (2) BOL; 20804 (3) BOL; 23170 (2) BOL; 24003 (3) BOL; 29618 (4b) BOL; 31190 (4a) BOL; 33594 (4b) BOL; 34362 (4b) BOL.

Farnham in Bolus 5922 (5) BOL. K, PRE; in Bolus 5923 (4b) BOL. K, SAM; in MacOwan & Bolus 1376 (5) BM. BOL. G. K. P. PRE, SAM. UPS. ZT; in SAM 22018 (4b) SAM; (4a) BOL—Flugge-de Smidt (1) NBG—Fourcade 532 (3) GRA; 2826 (3) K, STE; (3) STE—Fries, Norlindh & Weimarck 281 (2) K—Froemling 567 (3) SAM—Fry in Herb. Galpin 4991 (2) PRE.

Galpin 3004 (2) PRE; 4625 (4b) PRE; 4626 (3) BOL. GRA. K. PRE; 4627 (3) PRE; 4991 (2) PRE—Garabedian in SAM 51404 (2) SAM; (1) K—Garside 49 (4b) K—Gillett 123 (2) BOL; 164 (2) BOL; 239 (2) BOL; 858 (4b) BOL; 1346 (3) BOL; 1790 (4b) BOL—

Goldblatt 420 (4b) BOL—Grant 2318 (2) PRE; 2330 (6) BOL, M, PRE; 2447 (1) K; 2448 (5) BR, PRE—Grey (1) K—Guthrie 1074 (1) NBG; 2460 (4b) NBG, SAM; 2461 (2) NBG; 2462 (2) BOL, NBG; 2463 (4b) NBG, SAM; (1) NBG—Guthrie & Page (2) PRE. Häfstrom & Acocks 369 (1) S; 370 (2) S—Häfstrom & Lindeberg (3) S—Hall 1044 (1) BOL; 1051 (5) BOL; 1193 (3) BOL—Hallack in Herb. Galpin 3004 (2) K, PRE—Hane-korn 708 (1) K, PRE; 709 (2) K, PRE, STE—Harvey (4a) K—Haynes 394 (4b) STE; 471 (3) STE—Haynes-Palmer in CH 57629 (2) NBG—Henderson 11979 (2) BOL; in CH 57619 (1) NBG—Henrici 3818 (1) PRE—Hesse 10 (4b) BOL, K—Holland (2) K—Hutchinson 584 (4b) BOL, K; 798 (3) K; 1014 (3) K; 1210 (3) K.

Immelman 256 (1) BOL.

Jeppe in PRE 33430 (2) PRE; (3) PRE.

Kassner 1219 (1) P; 1481 (1) P—Keet (5) STE—Kerfoot 5373 (4b) BOL; 5889 (2) NBG; 5962 (3) NBG—Kies in CH 57631 (3) NBG—Knobel in PRE 22923 (2) PRE—Kruger 546 (3) STE; 1080 (4b) STE.

Leighton 2159 (3) BOL; 2292 (3) BOL; 3024 (2) BOL—Leipoldt 909 (3) BOL, NBG; 928 (1) BOL; 3204 (5) BOL; 3808 (1) BOL; 4074 (5) BOL; (3) BOL; (4b) BOL; (5) BOL; (5) BOL—Lewis 107 (4a) SAM; 708 (3) SAM; 723 (4a) SAM; 872 (3) SAM; 1649 (4b) SAM; 1831 (4a) SAM; 2336 (4b) SAM; 2337 (5) SAM; 2678 (2) SAM; 2679 (1) SAM; 3555 (4b) SAM; 4751 (1) SAM; 5642 (3) NBG; 5717 (5) NBG; 5871 (5) NBG; 6053 (1) NBG; 22272 (3) BOL; (1) BOL; (1) BOL; (2) BOL; (3) BOL—Liebenberg (5) STE—Linder 471 (3) BOL; 472 (3) BOL; 574 (3) BOL; 575 (2) BOL; 576 (2) BOL; 577 (4b) BOL; 578 (3) BOL—Linley in SAM 49373 (4b) SAM; Linley in SAM 49375 (2) PRE, SAM; in SAM 56095 (1) SAM; in SAM 56522 (4a) PRE, SAM; in SAM 59666 (3) SAM—Long 1405 (2) BOL.

MacOwan 172 (1) BOL, SAM; in STE 13004 (4b) STE; (4a) GRA—MacOwan & Bolus 172 (1) BM, G, GRA, K, UPS, ZT; 173 (4a) BM, BOL, G, K, SAM, UPS, ZT; 1375 (3) BM, G, K, P, PRE, SAM, ZT; 1376 (5) BM, BOL, G, K, P, PRE, SAM, UPS, ZT—Maguire 173 (5) NBG—Mann 11371 (2) PRE—Marais (1) STE—Markotter (2) STE—Marloth 1825 (3) PRE; 1894 (3) PRE; 7034 (4b) PRE; 7036 (2) PRE; 7104 (5) PRE; 7105 (1) PRE; 10566 (2) PRE; 10621 (1) PRE; 10673 (3) PRE—Marsh 552 (2) STE—Middlemost 2211 (2) STE—Morrison (1) STE—Muir 675 (2) PRE; 803 (3) BOL, PRE, SAM; (3) BOL—Mund (3) G, GRA.

Oliver 1341 (2) STE; 3031 (3) STE; 3498 (2) PRE; 4023 (1) K, PRE, STE; 4031 (1) PRE, STE; 5083 (3) K, STE; 5084 (1) STE; 5166 (1) STE.

Pappe in SAM 22013 (1) K, P, SAM; in SAM 22020 (4b) SAM; (4a) SAM—Paterson 1142 (2) BOL; in PRE 25796 (2) PRE—Penther 192 (5) PRE; 256 (5) BM—Phillips 1859 (3) SAM; 7561 (1) BOL, K, PRE, SAM, STE—Phillipson 1405 (3) K—Pillans 7303 (3) BOL; 7835 (2) BOL—Pocock 160 (3) PRE, STE—Pole-Evans 4267 (3) PRE—Powrie 167 (3) BOL—Prentice in Bolus 13900 (4b) BOL; in Marloth 7034 (4b) PRE—Primos 102 (3) PRE.

Rehman 29 (3) BM, Z; 569 (4a) Z; 2223 (5) Z; 5854 (3) Z—Ringgold & Rogers 132 (4a) K—Roberts (4b) PRE—Roberts & Adendorff in PRE 17623 (4b) PRE; (1) PRE—Rogers 3038 (2) G; 16590 (2) G; 17876 (3) Z—Roxburgh (1) BM—Rycroft 2556 (1) M, NBG.

Salter 1290 (2) BM; 4681 (5) BM, BOL, K; 4724 (2) BM, BOL, K; 4732 (6) BM, BOL, K; 4741 (4b) BOL; 4742 (4b) BM; 6215 (4b) BOL; 6281 (4a) BOL; 8471 (4a) BOL; 325/11 (4a) BM, K; in SAM 53007 (4a) SAM—Sanderson 929 (5) K; 930 (2) K—Schelpe 4142 (5) BM; 4885 (4b) BOL; 7116 (3) BOL—Schlechter 123 (3) BM, GRA, P, PRE, Z; 171 (3) Z; 1144 (4b) BM, G, GRA, K, M, PRE, SAM, Z; 1175 (2) BM, BOL, G, GRA, K, M, W, Z; 1314 (4a) BM, G, GRA, K, Z; 1375 (3) SAM; 1433 (4b) BM, BR, GRA, K, Z; 1463 (4a) Z; 1551 (4a) Z; 1661 (1) GRA, Z; 5012 (5) BOL, GRA, Z; 5103 (5) BM, BOL, BR, G, GRA, K, P, PRE, STE, UPS, Z; 5248 (6) BM, BOL, BR, PRE, S, SAM; 5386 (4b) BM, G, GRA, K, PRE, Z; 5414 (3) Z; 5488 (3) BM, G, GRA, K, PRE, Z; 7894 (5) BM, G, GRA, K, P, PRE, Z; (3) PRE—Schroeter (1) ZT—Scully (1) SAM; (4b) BOL, Z—Seligman (3) BM—Sidey 1857 (1) PRE, S; 2296 (4a) S—Sieber (1) P—Skinner 2

(3) GRA—Smith 24 (4b) STE—Stauffer & Oliver 5091 (4b) G, K, Z; 5108 (4a) Z—Steyn 356 (2) NBG; 656 (4a) SAM—Stokoe 1109 (3) PRE; 8924 (4b) BOL; 10566a (3) PRE; in Marloth 10566 (2) PRE; in SAM 49374 (4b) SAM; in SAM 49375 (4b) SAM; in SAM 49377 (3) SAM; in SAM 55876 (3) SAM; in SAM 56872 (4b) SAM; in SAM 57987 (4b) SAM; in SAM 57988 (4b) SAM; in SAM 59665 (4b) SAM; in SAM 60133 (5) SAM; in SAM 60399 (4b) SAM; in SAM 61030 (4b) SAM; in SAM 61032 (3); in SAM 61035 (5) SAM; in SAM 63144 (3) SAM; in SAM 63772 (2) SAM; in SAM 68582 (2) SAM; (2) BOL; (3) STE—Strauss 45 (3) NBG; 49 (3) NBG; 54 (1) NBG, Strey 530 (4b) PRE; 589 (1) PRE; 831 (2) PRE—Swart in STE 11153 (4b) STE.

Taylor 243 (3) BOL; 982 (3) SAM; 1003 (3) SAM; 4945 (4b) STE; 5824 (4b) STE—Thode 1027 (3) K, PRE; 2073 (3) PRE; 2594 (2) PRE; 5425 (4a) STE; 8162 (4a) STE—Thomas in CH 62762 (1) NBG—Thorne in SAM 38964 (3) SAM; in SAM 46510 (3) SAM—Thunberg 21466 (3) UPS—Thurling & Neil (5) PRE—Trimen (1) BM; (2) BM—Tyson 642a (4b) GRA; 642b (3) GRA; 642c (6) GRA; 642 (1) BOL, SAM.

Van der Merwe 992 (5) PRE—Van Niekerk 305 (4b) NBG, SAM; 306 (2) NBG; 632 (5) BOL—Van Staden 11 (3) PRE—Verdoucq 26 (4b) STE—Verreaux (1) G—Viljoen in STE 11515 (4b) STE.

Wahlberg (3) S—Walgate 401 (1) NBG—Wall (1) S; (3) S; (5) S; (4a) S—Wasserfall 373 (2) NBG; 373a (2) NBG; 515 (3) NBG; 603 (3) NBG—Werdermann & Oberdieck 896 (3) PRE; 986 (3) PRE; 8646 (3) PRE—West (2) GRA—Wilms 3662 (4a) BM, K, P—Wolley-Dodd 496 (1) K; 606 (4a) BM, BOL, K; 1291 (4a) BM; 1489 (4a) BOL; 1896 (4a) K; 2125 (3) BM, BOL, K; 2746 (4a) BOL, K; in SAM 51403 (2) SAM—Worsdell (1) K; (4b) K—Wurts 1068 (2) NBG; 1069 (3) NBG; 1429 (2) NBG.

Zeyher 372 (4a) K; 419 (1) P; 1571 (4a) BOL, G, K, P, PRE, S, Z; 3927 (1) BM, PRE; 3928 (5) BM, K, P, PRE, S, SAM, Z; 3929 (2) BM, K, S, W; 3930 (4b) BM, K, P, SAM; in SAM 22007 (1) K, SAM; in SAM 22015 (3) K, SAM; (4a) SAM.

STUDIES IN THE GENERA OF THE *DIOSMEAE* (RUTACEAE): 11. A REVIEW OF THE GENUS *MACROSTYLIS*

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ABSTRACT

The ten species belonging to the genus *Macrostylis* Bartl. & Wendl. are listed with diagnoses and keys. Species not recently published are described from fresh material with up-to-date distribution maps and with lists of specimens examined.

UITTREKSEL

STUDIES IN DIE GENERA VAN DIE *DIOSMEAE* (RUTACEAE): 11. 'N OORSIG VAN DIE GENUS *MACROSTYLIS*

Die tien soorte van die geslag *Macrostylis* Bartl. & Wendl. met diagnose en sleutels word gekatalogiseer. Soorte nie onlangs gepubliseer nie word van vars materiaal beskryf, met die jongste verspreidingskaarte en met 'n lys van die soorte ondersoek.

HISTORICAL BACKGROUND

The generic name *Macrostylis*, meaning large or lengthy style, was proposed by Bartling & Wendland in their revision of the *Diosmeae* published in 1824. Of the four species enumerated by them, *M. barbiger* and *M. squarrosa* have been maintained, *M. lanceolata* has been placed in synonymy under *M. villosa* (Thunb.) Sonder and *M. obtusa* in synonymy under *M. squarrosa*.

Sonder in his revision of the Rutaceae for the *Flora Capensis* (1860) recognised eight species in the genus *Macrostylis* two of which, as mentioned above, had been previously published. He validated three manuscript names, *M. decipiens*, *M. tenuis* and *M. hirta* of E. Meyer published in Drège's *Zwei Pflanzengeographische Documente* (1844), made the new combination *M. villosa* (Thunb.) Sonder, and proposed two new names *M. crassifolia* and *M. ovata*. Of these *M. crassifolia* has been maintained and *M. ovata*, based on a single fragment collected by Niven, has been considered to be conspecific with *M. tenuis*, a very variable species.

As mentioned under *Euchaetis* (Williams, Jl S. Afr. Bot. 47: 1981) *E. dubia* Sond. was transferred to *Macrostylis* under the name *M. cassiopoides* (Turcz.) Williams. The name *M. cauliflora* Williams, for a small plant from the Bredasdorp Division, was published in the *Journal of South African Botany* (1975) bringing the total number of species recognised in the genus to ten.

Accepted for publication 3rd July, 1980.

Two species have been excluded. They are *M. cordata* G. Don and *M. pater-soniae* Schonland.

GENERIC DESCRIPTION

Macrostylis Bartl. & Wendl. *Diosmeae* in Beitr. Bot. **1**: 191 (1824); A. Juss. in Mém. Mus. Hist. Nat., Paris **13**: 476 (1825); Don, Gard. and Bot. **1**: 789 (1831); Eckl. & Zeyh., Enum. Plant.: 104 (1835); Endl., Gen. Plant. **2**: 1158 (1840); Lindl., Veg. Kingd.: 471 (1853); Sond. in Flor. Cap. **1**: 439 (1860); Benth. & Hook., Gen. Plant. **1**: 289 (1862–1867); Engl., Pflanzenfam. **19a**: 276 (1931); Dyer, Gen. S. Afr. Flow. Pl. **1**: 292 (1975). Type species: *M. barbiger*a (L.f.) Bartl. & Wendl. *Diosma* L.f. Suppl. Plant.: 155 (1781).

Shrubs 0.2–1.5 m tall, usually about 0.3 m, often forming a dense bush light green in colour, either arising from a single stem at base or with several stems coppicing after fires.

Branches short, slender, erect or variously bent, glabrescent. *Branchlets* short, slender, often puberulous. *Leaves* 2–13 mm long, subulate, lanceolate, ovate, elliptic, or cordate, adpressed or spreading, usually alternate, in one case only opposite, ciliate, ciliolate or eciliate, sessile or in one case only (*M. villosa*) with a very short petiole. *Inflorescence* terminal, 1–14 aggregate, usually 5–8 aggregate, in one case (*M. barbiger*a) pedunculate; *flowers* white or creamy-white, very small, subtended by one bract and two bracteoles, usually sessile. *Calyx* five-lobed, persisting if fertile. *Petals* crisp-bearded about the middle, sometimes sparsely ciliate towards the middle at the sides. *Staminodes* five, vestigial, in one case only (*M. cassiopoides*) as much as 0.7 mm long. *Filaments* five, becoming 3 to 9 mm long, carrying the spent anthers beyond the petals,

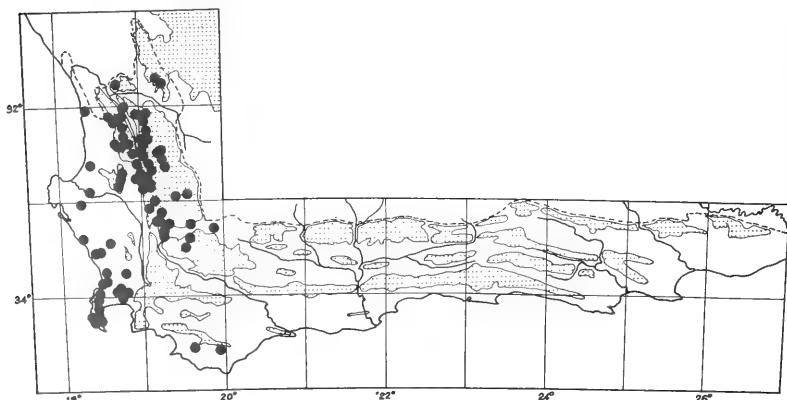


FIG. 1.
Distribution of the genus *Macrostylis*.

glabrous. *Anthers* five, dorsifixed; apical gland globose, minute, usually sessile. *Pollen* 44–63 μ long, 18–30 μ broad, ellipsoid, sticky, triporate. *Disc* envelops the ovary, nectariferous. *Stigma* simple or in two cases (*M. cassiopoides* and *M. cauliflora*) capitellate. *Style* becoming 3.5–9 mm long, usually exceeding the petals by a long way, glabrous, filiform. *Ovary* usually 3-carpellate, in 2 species 3 or 4-carpellate and in one species 2–3 carpellate, 0.5–0.8 mm long, 0.4–0.7 mm diam., glabrous. *Fruit* normally 3-carpellate with only 1 or 2 developing; in *M. cassiopoides* and *M. hirta* 3 or 4-carpellate and in *M. tenuis* 2 or 3-carpellate; *horns* 3–5 mm long except for *M. cassiopoides* where 1.5 mm long and *M. cauliflora* where 2 mm long. *Seed* 5–7.6 mm long, including the white aril adjacent to the truncated apex, 1.8–2.5 mm broad, black, mottled, matt except in the case of *M. cassiopoides* where black, shining.

Characters which definitely place a plant in the genus *Macrostylis* are: fruit apocarpous; flowers complete; petals crisp-bearded beyond which the filaments and style ultimately protrude; filaments and style glabrous and lengthening greatly; anthers with a very small, usually globose, apical gland; staminodes vestigial, in one case only 0.7 mm long; disc closing over the ovary to the base of the style; ovary 2, 3 or 4-carpellate.

It should be noted that the beard on the petals in *Macrostylis* consists of a patch of crisped pubescence about the middle of the petal. *Euchaetis* is the only other genus with characteristically bearded petals. Here however the beard is in the form of a transverse fringe of hairs which together with the ciliate margins on the petals form a cage beyond which the stigma and anthers never protrude.

DISTRIBUTION

The genus *Macrostylis* is found only in the South Western Cape, approximately to the west of 20° longitude; i.e. from Bredasdorp in the east to the Atlantic coast in the west and from near Elim and Bredasdorp in the south to Lokenberg and the Giftberg in the north near Vanrhynsdorp. A discontinuity of about 135 km exists between populations found on the Cape Flats and those in the Bredasdorp Division.

KEY TO SPECIES OF *MACROSTYLIS*

1	Stigma capitellate, 0.3–0.4 mm in diam.	2
1+	Stigma simple	3
2	Leaves 5 mm long, lanceolate, acute	1. <i>cassiopoides</i>
2+	Leaves 2.5 mm long, elliptic, obtuse	6. <i>cauliflora</i>
3	Leaves lanceolate or subulate, acute	4
3+	Leaves elliptic, ovate or oblong, obtuse, subacute or cuspidate	6
4	Leaves lanceolate, acute, apex trunculate	5
4+	Leaves subulate, acute, apex blunt and hairy	3. <i>ramulosa</i>
5	Leaves 4–13 mm long	2. <i>villosa</i>
5+	Leaves 4–6 mm long	4. <i>decipiens</i>
6	Leaves elliptic, obtuse	7

6 ⁺	Leaves ovate, oblong-ovate, cordate, obtuse sub-acute or cuspidate	8
7	Leaves adpressed, thin at base, margins serrulate and narrowly cartilagenous	5. <i>tenuis</i>
7 ⁺	Leaves spreading, thick at base, margins thick midrib broad and prominent	8. <i>crassifolia</i>
8	Leaves ovate or oblong-ovate, obtuse	9
8 ⁺	Leaves ovate, sub-acute or cuspidate	10
9	Leaves strongly recurved, fruit 3-carpellate	7. <i>squarrosa</i>
9 ⁺	Leaves not strongly recurved, fruit often 2-carpellate	5. <i>tenuis</i>
10	Leaves 6–12 mm long, ovate, cordate, cuspidate	10. <i>barbigera</i>
10 ⁺	Leaves less than 6 mm long, ovate, cordate sub-acute	9. <i>hirta</i>

1. *Macrostylis cassiopoides* (Turcz.) Williams in Jl S. Afr. Bot. **47** (2): 192 (1981).

Acmadenia cassiopoides Turcz. in Bull. Soc. Imp. Nat. Mosc. **31**: 1: 439 (1858). Type: Lang Valley, Zeyher 291 (BM, G, K, LD, MEL, P, PRE, S, SAM, W). The whereabouts of the specimen seen by Turczaninov is unknown.

Euchaetis dubia Sond. in Flor. Cap. **1**: 373 (1860). Type: as above.

Euchaetis dubia Sond. var *pauciflora* Sond. in Flor. Cap. **1**: 373 (1860). Type: Ratelklip, alt. 2, June. Zeyher 292 (G, K, MEL, P, PRE, SAM).

Macrostylis dubia Benth. and Hook. Gen. Plant. **1**: 289 (1862–1867) nom. nud.

Shrubs up to 1,5 m tall, erect, slender, single-stemmed at base with a long tap root. *Branches* erect, slender, becoming leafless, glabrous with a finely roughened grey bark. *Branchlets* numerous, erect, very slender, dichotomous, glabrous, well clothed with leaves. *Leaves* up to 7 mm long on healthy young plants, otherwise 3–5 mm long, 1,2–1,3 mm broad, lanceolate, sub-acute with a blunt point, glabrous, adpressed, erect, longer than the internodes, imbricate on new shoots, sessile-decurrent, alternate; adaxial surface concave, waxy; abaxial surface convex with scattered gland dots, sub-scabrid with minute white glands; margins narrowly cartilagenous, sparsely ciliate towards the base. *Inflorescence* terminal, 1–5 aggregate, sessile. *Bract* 1,7 mm long, 1,2 mm broad, oblong, obtuse with a blunt reddened tip; margins broadly translucent, densely ciliate; midrib thickened, glabrous, gland-dotted; adaxial surface concave, pubescent in the upper half towards the middle. *Bracteoles* two, 1,8–2,0 mm long, 1 mm broad, elliptic, narrowed at the base, obtuse; midrib thickened, glabrous, gland-dotted with a blunt tip; margins broadly translucent, densely ciliate; adaxial surface concave, sparsely pubescent in the upper half towards the middle. *Calyx lobes* five, 2 mm long, 1,8 mm broad, orbicular; margins broadly translucent, ciliate; abaxial surface glabrous with the midrib somewhat reddened, gland-dotted; adaxial surface concave, densely pubescent towards the centre in the upper two thirds. *Petals* five, 4 mm long overall, white; *limb* 1,4 mm diam., orbicular, margin irregular in outline; *claw* 2,6 mm long, 1,1 mm broad, densely bearded mainly down the midrib, crisped ciliate above. *Staminodes* five, 0,6–0,7

mm long, glabrous. *Filaments* five, becoming 3 mm long, glabrous. *Anthers* 1.1 mm long, 0.7 mm broad, reddened; apical gland 0.3 mm long, short-stipitate. *Pollen* 60 μ long, 25–27 μ broad, elliptic or oblong. *Disc* closes over the ovary clasping the style, smooth, green, exudes nectar from pores on the domed surface. *Stigma* 0.4 mm diam., capitate, green. *Style* 0.4 mm diam. at first, becoming 3.5 mm long, exceeding the beards of the petals, glabrous, erect, persisting. *Ovary* 0.8 mm long, 0.7 mm diam., tri-carpellate, glabrous. *Fruit* 3 or rarely 4-carpellate, 8–8.5 mm long, brownish-red, pitted with gland dots, horns very short, erect, emarginate. *Seed* 5.5 mm long including the white aril, 1.8 mm broad, black, shining.

In proposing the name *E. dubia*, Sonder was apparently unaware of the prior publication of the name *Acmadenia cassiopoides* by Turczaninov in 1858. Sonder remarked that his *Euchaetis dubia* was "a doubtful member of the present genus, approaching *Macrostylis*, in the stamens, the style not elongating, nor more slender at the base, and in the capitate stigma". From the poor quality of the material available it could not be seen that the style does in fact elongate and that the filaments also thrust the spent anthers beyond the petals at the sides.

Turczaninov who worked upon the same collection, containing immature flowers (Zeyher 291), also could not observe that the style might lengthen and,

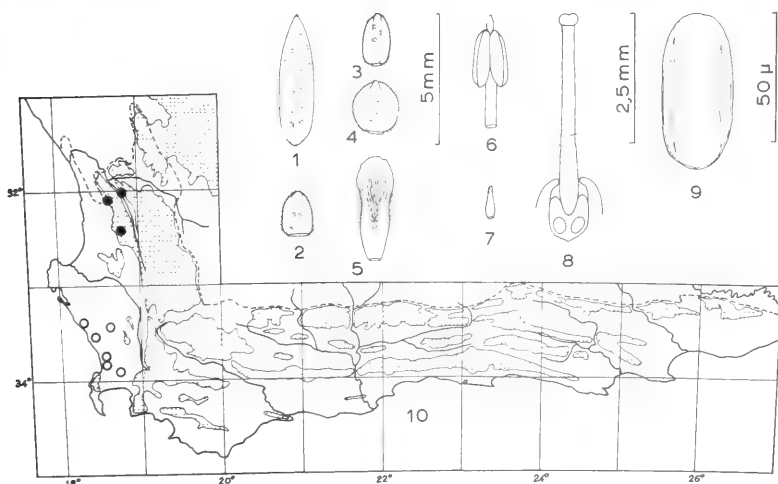


FIG. 2.

Macrostylis cassiopoides: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, staminode. 8, gynoecium and disc. 9, pollen. 10, distribution; open circles: subsp. *dregeana*.

noting the presence of staminodes, placed it in the genus *Acmadenia* remarking "Stamens not projecting, the sterile filaments without glands as long as the fertile."

In assigning this species to the genus *Macrostylis* the following characters are taken into account:—1) the beard on the petal is not strictly a transverse beard but also very broad running up and down the petal; 2) the style and filaments eventually become sufficiently lengthened to place the stigma and anthers above the beard equalling the tips of the petals; 3) the disc closes over the ovary encircling the base of the style. The above description made from fresh material, collected from near the type locality (Williams 2011), amplifies those previously published.

SPECIMENS EXAMINED

CAPE—3218 (Clanwilliam): in arenosis ad Langvallei, Clanwilliam Division, -/1/-, Zeyher 291 (BM, G, K, LD, MEL, P, PRE, S, SAM, W); ad Ratelklip in arenosis, -/6/-, Zeyher 292 (G, K, MEL, P, PRE, S, SAM); Nardouw Kloof, Clanwilliam Division (-BB), -/9/1947, *Stokoe s.n.* (SAM 64146); Sandy uplands N. of Paliesheuvel between Bergvallei and Langvallei, Clanwilliam Division (-BD), 23/9/1934, *Acock* 2923 (S); Bergvalley/Swartbaskraal boundary, 3 km E. of Main Road, 1 300 ft., 11/7/1975, *Williams* 2011 (NBG), 16/11/1977, *Williams* 2396 (NBG).

DISTRIBUTION

Macrostylis cassiopoides subsp. *cassiopoides* appears to be extremely rare having been very seldom collected and then only in four localities. The two localities, Nardouws Kloof and Bergvalley, are about 45 km apart in a north-south direction. Still further to the south, after a discontinuity of about 112 km, one begins to find populations of *M. cassiopoides* subsp. *dregeana* which once extended from near Darling southwards to Stickland near Bellville. This subspecies has also been very seldom collected. The fact that the plants are very slender and diffuse with very insignificant flowers may help to explain this apparent appearance of rarity. Miss E. Esterhuysen (32583) reported seeing it for 20 miles, wherever the fynbos had not been disturbed, along the main road to Malmesbury.

Macrostylis cassiopoides subsp. *cassiopoides* is recognised as distinct being a slender shrub up to 1.5 m tall single-stemmed at base, with branchlets glabrous and leaves closely adpressed, with staminodes, 0.6 mm long, having the anther with a small stalked apical gland, the stigma 0.4 mm diam., capitate, and the fruit 3 or 4-carpellate with short horns. It differs from subsp. *dregeana* which has branchlets puberulous, leaves ciliate with a broader hyaline margin, petals with a narrow blade, staminodes 0.4 mm long and the anther with a much smaller apical gland.

4a. *Macrostylis cassiopoides* subsp. *dregeana* (Sond.) Williams, stat. nov. et comb. nov. Type: between Paardeneiland, Blauwberg and Tygerberg, sandy plain, below 500 ft., May to Aug., Drège 7111 (S, lectotype; MEL, isoelecto-type).

Euchaetis dubia var. *dregeana* Sond. in Flor. Cap. 1: 373 (1860). Type: as above.

Shrubs up to 0.7 m tall, erect, slender, single-stemmed at base. *Branches* erect, slender, glabrous, fairly smooth, dichotomous. *Branchlets* erect, very slender, puberulous, densely clothed with leaves. *Leaves* about 5 mm long, 1 mm broad, lanceolate, glabrous, adpressed, clasping, erect, sessile, somewhat decurrent, normally alternate; apex sub-acute, callused; margins narrowly translucent, ciliate at first; adaxially concave with waxy glands; abaxially convex, gland-dotted. *Inflorescence* terminal, 4-aggregate, sessile. *Bract* 2.3 mm long, 1.3 mm broad, broadly lanceolate, glabrous; apex with a blunt callus; margins ciliate, translucent; adaxially sparsely pubescent. *Bracteoles* two, 2 mm long, 0.8 mm broad, asymmetrically lanceolate, glabrous; apex callused; margins densely ciliate, translucent; adaxially pubescent. *Calyx lobes* five, 2.3 mm long, 1.7 mm broad, ovate, glabrous, apex thickened, obtuse; margins broadly translucent, ciliate; adaxially pubescent. *Petals* five, 3.3 mm long; limb 1.2 mm broad; claw 0.8 mm broad, very densely bearded above and on the upper part of the midrib, ciliate above. *Staminodes* five, 0.4 mm long, clavate. *Filaments* five, becoming 2 mm long and carrying the spent anthers outside the petals, glabrous. *Anthers* five, 1 mm long, 0.5 mm broad, yellow; apical gland globose 0.1 mm diam. *Pollen* 43 μ long, 22 μ broad, oblong. *Disc* closes over the ovary, exudes nectar. *Stigma* 0.3 mm diam., capitellate. *Style* becoming 2 mm long, glabrous, erect, persisting. *Ovary* 4-carpellate, 0.5 mm diam., glabrous. *Fruit* 4-carpellate, 6 mm long, 4 mm diam., glabrous; horns 1.5 mm long, emarginate, erect. *Seed* 4–4.5 mm long, 1.5 mm broad, black, shining.

In his *Zwei Pflanzengeographische Documente* (1844) Drège placed his number 7111 under *Agathosma* and, no doubt, distributed duplicates to herbaria which have escaped the notice of the author. The specimens cited above were both from Sonder's herbarium and were seen by him. The above description, which amplifies that of Sonder, was done from fresh material (*Williams 1746*).

SPECIMENS EXAMINED

—3318 (Cape Town): Lay by 3.4 km S. of Ysterfontein Road on new road to Saldanha Bay, Malmesbury Division (–AD), 280 ft., 6/2/1977, *Williams 2410* (NBG); Preekstool, Malmesbury Division (–BC), 8/4/1976, *Esterhuysen 34234* (BOL); Mamre Flats, Malmesbury Division (–CB), –/3/1940, *Penfold 245* (NBG); along the old road from Cape Town to Malmesbury near the turn off to Mamre, Cape Division (–DC), 11/11/1970, *Esterhuysen 32530* (BOL); National Road to Malmesbury at junction with Darling Road, 17 miles from Cape Town,

Cape/Malmesbury Division, 230 ft., 17/1/1973, *Williams 1746* (NBG); near Bothasig along the road to Malmesbury, Cape Division, 19/3/1971, *Esterhuysen 32583* (BOL); Monte Vista, Cape Division, 20/10/1965, *Esterhuysen 31300* (BOL); Flats near Stickland, Cape Division, 30/3/1933, *Acock s.n.* (SAM).

2. *Macrostylis villosa* (Thunb.) Sonder subsp. ***villosa*** in Flor. Cap. **1**: 439 (1860). Type: *Diosma villosa*. α . 146 *Thunberg s.n.* (UPS-THUNB 5724, holotype; LINN 270/20, S, isotypes).

Diosma villosa Thunb. Prodr. Plant. Cap.: 43 (1974). Type: as above.

Macrostylis villosa (Thunb.) Sond. var *B. glabrata* Sonder loc. sit. Type: includes *M. lanceolata* Bartl. & Wendl.

Macrostylis lanceolata Bartling & Wendland, Diosmeae in Beitr. Bot. **1**: 194 (1824) excl. syns. Type: Habitat in Africa maxime australi. *Hesse s.n.* (G, GOET-W)

Macrostylis sieberi? Turcz. in Bull. Soc. Imp. Nat. Mosc. **31**: 1: 439 (1858). Type: Inter planta Siberianas absque schedula. (Note: the only species of *Macrostylis* collected by Sieber at (W) Vienna is *M. villosa*).

Macrostylis barbata St Hil. ex Steud Nom. Bot. Ed 2. **2**: 89 (1841) nom. nud.

Not *Agathosma barbatum* Spreng. pugill. **1**: 20 (1813) which is *Agathosma*.

Not *Bucco barbata* Roem. et Schult. Syst. Veg. **5**: 445 (1819). which is *Agathosma*.

Shrubs about 0,3 m tall with several stems arising from a stout woody underground rootstock. *Stems* erect, slender, glabrous. *Branchlets* erect, slender, short, somewhat reddened, puberulous, well-clothed with leaves. *Leaves* 4–13 mm long, 2 mm broad, lanceolate, acute, rounded and short-petiolate at the base, erect, crowded, somewhat imbricate, alternate; apex triquetrous, somewhat truncate; adaxially flattish, glabrous; abaxial surface glabrous or pubescent with a prominent gland-dotted midrib; margins quite thick, eciliate or crisped ciliate, gland-dotted. *Inflorescence* terminal, umbellate-capitate, 11–14 flowered; buds pink; petals white, spreading, conspicuous. *Bract* one per flower, outermost leaflike, inner much reduced, 1,5 mm long, 0,6 mm broad, lanceolate, glabrous or crisped pubescent; apex truncate; margins sparsely ciliate or crisped ciliate. *Bracteoles* two at the base of the pedicel, 1 mm long, 0,7 mm wide, ovate, ciliate; margins translucent; midrib thickened. *Pedicel* about 2 mm long, glabrous. *Calyx lobes* five, 1,8–2,7 mm long, 1 mm broad, lanceolate; apex truncate; midrib prominent, glabrous or crisped pubescent; margins translucent, ciliate. *Petals* five, 5,8 mm long overall; *limb* 1,6 mm broad, irregularly orbicular, recurved; *claw* 1,2 mm broad, narrowing below, eciliate, strongly crisp-bearded above becoming shorter pubescent below. *Staminal nodes* five, 0,15 mm long, a minute scale against the outside of the disc at the base of the petal. *Filaments* five, becoming 9 mm long, glabrous, exerted. *Anthers* five, before anthesis 1,3 mm long, 0,7 mm broad, reddened; apical

gland globose, minute. Pollen 56 μ long, 25 μ diam., oblong. Disc closed over the ovary, bright green, exudes nectar. Stigma 0.2 mm diam., globose, capitate. Style becoming 10 mm long, glabrous, very slightly narrowed below. Ovary 3-carpellate, 0.7 mm diam., glabrous. Fruit 3-carpellate, only one or two may develop, about 13 mm long overall including the pedicel 1 mm long, glabrous, green or tinged with purple; horn 4–5 mm long, erect. Seed 4.5–6 mm long with the white aril extending a further 1.5 mm at the apex, black, matt, mottled.

C. P. Thunberg collected this plant at the Cape round about 1772–1773 and a specimen labelled *Diosma villosa*. α . is preserved with his herbarium at Upsala. A brief description given by Thunberg in his *Prodromus* (1794) clearly refers to this plant. Under his supervision one of his students C. J. Pentz produced the *Dissertatio de Diosma* in 1797 in which he enlarged upon the brief diagnoses previously published by Thunberg. Referring to *Diosma villosa*, part of his description states *Nectararia quinque, barbata* (= Staminodes five, bearded). As this specimen has virtually no staminodes, Pentz may have mistaken its petals for staminodes or he may have been looking at some other plant. Although his error has no bearing on the validity of the name *M. villosa* (Thunb.) Sond. it may later have affected the thinking of others. For example Bartling & Wendland from this description placed *D. villosa* Thunb. doubtfully in synonymy with *Adenandra villosa*. Apparently they had not seen Thunberg's specimen.

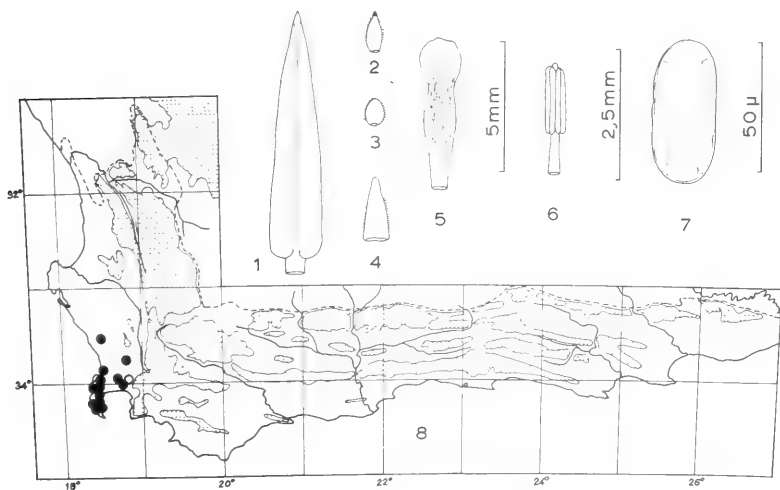


FIG. 3.

Macrostylis villosa: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, pollen. 8, distribution; open circle: subspecies *minor*.

Sprengel (1813), without citing a type, named a plant *Agathosma barbatum* the identity of which can not easily be determined because Halle, where Sprengel worked, is now in East Germany. However as he mentions in his description that it has glabrous petals and bearded staminodes there can be no doubt at all that he refers to some species of *Agathosma* and not to a species of *Macrostylis* all of which have bearded petals and virtually no staminodes. Roemer & Schultes (1819) transferred this species to the genus *Bucco* as *Bucco barbata*; *Bucco* being a synonym for *Agathosma*. When Bartling and Wendland (1824) proposed the name *Macrostylis lanceolata* they, apparently in error, cited *Agathosma barbatum* and *Bucco barbata* as synonyms.

Sonder, having seen the specimens in Thunberg's herbarium, was in no doubt that *M. villosa* (Thunb.) Sond. was the correct name for this plant and placed *M. lanceolata* B. & W. in synonymy with his var. β . *glabrata*. However he still seemed quite happy to keep *Agathosma barbata* Spreng. and *Bucco barbata* R. & S. in synonymy with his *M. villosa*. This probably led Pillans (1950) to equate *Agathosma barbata* Spreng. with *M. villosa* Sond. which error is perpetuated by Strid (1972) who stated that *Diosma villosa* α & β in Thunberg's herbarium is a species of *Agathosma*.

With regard to specimen number 270/20 in Herb. LINN, it may be of interest to note that, preserved at the Linnaean Society in London, is a slip of paper upon which Linnaeus wrote a description of *Diosma barbiflora* based upon this specimen of *Macrostylis villosa* which he had received from Thunberg. He had intended that this description should be published together with others written upon similar slips of paper, including that of *D. barbiger*a. However Linnaeus' son, apparently confusing it with *D. barbiger*a, crossed it all out so that it failed to appear in the *Supplementum Plantarum* (1781) and the Linnaean name was unfortunately never validated.

The variation in pubescence, noted by Sonder, is apparently of no taxonomic significance and so Sonder's var. β *glabrata* is therefore placed in synonymy. The above description done from fresh material amplifies those of previous authors.

SPECIMENS EXAMINED

CAPE—3318 (Cape Town): near Melkbosstrand, Malmesbury Division (—CB), 25/11/1951, *Maguire 1726* (NBG); road to Pella near Mamre, Malmesbury Division, 700 ft., 17/1/1973, *Williams 1745* (NBG), 25/1/1977, *Williams 2266* (NBG); Cape Flats near Claremont, Cape Division, (—CD), 7/3/1896, *Wolley Dod 994* (BM, BOL, K), 24/2/1892, *Schlechter 404* (C); Kirstenbosch, slopes north of Window Stream, —/5/1946, *Esterhuysen s.n.* (BOL), 28/9/1947, *Esterhuysen 14057* (BOL), 4/6/1950, *Esterhuysen 17336* (BOL), 500 ft., 4/4/1956, *Esterhuysen 25566* (BOL); Hout Bay valley, slopes below Grootkop, 21/3/1942, *Esterhuysen 7795* (BOL), 21/3/1942, *Compton 13066* (NBG); near Cape Town, —/5/—, *Zeyher 86.5* (C, E, GOET, MEL, S, SAM), —/7/1856, *de Castlemain 450*

(P), 500 (P); Rondebosch flats, -/5/1882, *Tyson* 2744 (E, K, PRE, SAM), 15/5/1898, *Froembling* 786 (BOL-FOURC); Kenilworth Race Course, 1/7/1941, *Walgate* 261 (NBG); Kenilworth, 300 ft., -/3/1895, *Flanagan* 2457 (PRE); on the road between Storms grave and Luyaardsfontein, in the Cape Downs, Stellenbosch Division, (-DC), 12/4/1815, *Burchell* 8359 (K); flats between Duikervallei and Blaauwberg under 200 ft., Cape Division, (111, E, b, 6), 25/7/1826, *Drège* 139 (P, G, PRE, S, W); between Bottelary Road and Main line, Stellenbosch Division, -/2/1932, *Acock* 104 (S); between Brackenfell and Kraaifontein, Stellenbosch Division, 12/4/1977, *Burgers* 419 (Nat. Cons. Herb.); near Lyndoch Station, Stellenbosch Division (-DD), 24/2/1917, *Garside* 667 (K); Geometric Tortoise Reserve, Eensaanheid, Achter Paarl, Paarl Division, 12/4/1977, *Burgers* 425 (Nat. Cons. Herb.).

—3418 (Simonstown): in clivis montis Muizenberg pone Kalk Bay, Cape Division (-AB), 1 000 ft., -/—/1880, *H. Bolus* 4525 (BM, BOL, K, SAM); hills, Muizenberg, 22/12/1922, *Moss* 11242 (BM); in arenosis Muizenberg, 300 m, -/3/1885, *Marloth* 566 (PRE), *Zeyher s.n.* (SAM), -/8/1951, *Stokoe s.n.* (SAM 67237); sandy soil at foot of Muizenberg, -/3/1838, *Bunbury s.n.* (BM); Simons-town, 14/4/1853, *Andersson s.n.* (S); above Noahs Ark Battery, Simonstown, 27/2/1896, *Wolley Dod* 918 (BM, BOL, K); Red Hill, Simonstown, 4/5/1927, *Salter* 245/25 (BM), -/8/1938, *Esterhuysen s.n.* (BOL); mountains over Simons Bay, -/3/1838, *Elliot* 9 (G); Simons Bay, 11/1/1846, *Prior s.n.* (K), 500–1 000 ft., -/4/1887, *Thode* 8514 (STE); Wynberg, 80 ft., 29/2/1896, *Schlechter* 7535 (BM, G, GRA, K), -/2/—, *Roxburgh s.n.* (BM, G), 10/5/1847, *Alexander Prior s.n.* (K); on the flats by Wynberg under 200 ft., (111, E, b, 2), 3/8/1826, *Drège* 365 (P); in arenosis planitiei Capensis prope Wynberg, under 100 ft., -/5/1886, *MacOwan* 2744 (E, K, PRE, SAM); north slopes of Vlakkenberg, 300 m, 23/5/1926, *Andreae* 1117 (PRE, STE); sandy lower slopes at Tierbos, Hout Bay, 20/2/1935, *Acock* 4140 (S); flats, Plumstead and slopes, Claassenbosch, Table Mountain, 1 000 ft., -/3/—, *Lamb* 2646 (SAM); Glencairn, -/4/1950, *Stokoe s.n.* (SAM 64154), 15/4/1930, *Arbuthnot s.n.* (BOL), -/8/1935, *Walgate s.n.* (BOL); Kalk Bay mountains, 24/6/1930, *Hutchinson & Levyns s.n.* (K); Clovelly, 25/2/1940, *Penfold* 236 (NBG); Trappies Kop, 2/3/1941, *Walgate* 213 (NBG); Slangkop, 9/5/1942, *Bond* 1496 (NBG); in arenosis planitiei Capensis prope Princess Vley, -/3/1896, *MacOwan* 1711 (G, GRA, K, P, SAM, W); in the vicinity of Witteboom & Constantia, 25/7/1815, *Burchell* 8590 (K); Smitswinkel, -/4/1929, *Salter* 245/25A (BM), 23/1/1934, *Galpin* 12728 (K, PRE), 16/3/1936, *Cullett* 1495 (K), 26/4/1940, *Compton* 8716 (NBG), 16/3/1941, *Compton* 10637 (NBG); Olifantsbosch, 200 ft., 23/1/1934, *Compton* 4702 (BOL, NBG), 10/5/1946, *Barker* 4008 (NBG); Cape Point, 3/4/1922, *Wilson* SA90 & SA111 (PRE); on the road from Hottentots Holland station to Jonkers Valley (-BB), 30/3/1815, *Burchell* 8303 (K).

Without precise locality: *Harvey* 1096 (BM, BOL, MEL); *Bowie s.n.* (BM);

–/–/1771, *Banks s.n.* (BM, C, W); *Meuron* (B–W 4767/2); *Meuron* (B–W 4783), –/10/1898, *Guthrie s.n.* (BOL), *Hesse s.n.* (G), *Masson s.n.* (G), *Verreaux s.n.* (G), *Ecklon 35* (GOET), –/–/1885, *Forster s.n.* (K), *Grey s.n.* (K), *Harvey 182* (K), *Harvey 495* (K); *Thunberg 493* (LINN 270/20, UPS–THUNB 5724 & 5725, S); –/–/1838, *Lehmann s.n.* (P); *Niven s.n.* (S); *Sieber s.n.* (W); *Guinzis s.n.* (W); *Scholl s.n.* (W); in sabulosis fruticum planitiei Capensis prope Doornhoogde, Wynberg et Muysenberg (Cap), Apr. Maio., *Ecklon & Zeyher 817* (C, G, GOET, K, LD, MEL, P, PRE, S, SAM, W).

DISTRIBUTION AND VARIATION

Macrostylis villosa is found growing in sandy soil at altitudes of from 30 to 300 m above sea level on the Cape Peninsula and on the Cape Flats as far north as Mamre. Many of the areas where it once flourished are now covered by urbanisation or by alien vegetation. Variation appears to be confined to the degree of pubescence on the twigs and leaves. A rare plant, only once collected by Acocks on the gravelly and clayey soil on the lower north slopes of the Bottellary hills, matches *M. villosa* in all respects except that all parts are very much smaller in size. As no intermediates or hybrids have been found it has been given the rank of subspecies.

Macrostylis villosa is recognised as distinct being one of only two *Macrostylis* species that coppice after fires, having the stigma capitellate and having leaves lanceolate acute 4–13 mm long with the apex truncate.

2a. *Macrostylis villosa* (Thunb.) Sond. subsp. **minor** Williams, subsp. nov.

Type: gravelly and clayey soil on lower north slopes of Bottellary hills, –/5/1934, *Acock(s) 2654* (S).

Foliis ad 8 mm longis, planta in omnes partes parviores distinguitur.

Shrubs 100–150 mm tall with many slender stems arising from a persistent rootstock. *Branchlets* short, rough, glabrous, spreading. *Leaves* 8 mm long, 0.8 mm broad, narrowly lanceolate, acute, glabrous, glaucous, short-petiolate, alternate, spreading; apex truncate; margins rounded; abaxial surface gland-dotted along the margins and along the prominent midrib. *Inflorescence* terminal, umbellate-capitate, about 12 flowered. *Bract* outermost somewhat leaf-like, 4.5 mm long, 0.7 mm broad, innermost very much reduced. *Bracteoles* two at the base of the pedicel, 0.5 mm long, 0.3 mm broad, pale, somewhat ovate, glabrous, ciliolate. *Pedicel* 1.5 mm long, glabrous. *Calyx lobes* five, 1.3 mm long, 0.6 mm broad, lanceolate, acute, glabrous, minutely ciliolate. *Petals* 1.7 mm long overall; *limb* 0.7 mm broad, ovate; *claw* crisped bearded in the middle and down the midrib, strongly crisped ciliate. *Staminodes* five, 0.05 mm long at the base of the disc. *Filaments* five, becoming about 2 mm long, glabrous. *Disc* purplish,

envelops the ovary. *Stigma* capitellate. *Style* becoming 2.5 mm long, glabrous. *Ovary* tricarpellate, glabrous. The rest not seen.

SPECIMEN EXAMINED

As above.

DISTRIBUTION

So far this plant has only been collected once by J. P. H. Acock(s) on the north slopes of Bottellary Hills. This area is now under fairly intensive cultivation and, in spite of searches having been made, it has not been rediscovered. Its small size may be an adaptation by *M. villosa* subsp. *villosa* to a different habitat, i.e. from the normal deep sandy soil to a hard gravelly-clayey and perhaps much drier soil.

M. villosa subsp. *minor* is easily distinguished from *M. villosa* subsp. *villosa* in having leaves not longer than 8 mm and in being a plant much smaller in all respects.

3. *Macrostylis ramulosa* Williams in Jl S. Afr. Bot. **44**(4): 356 (1978). Type: CAPE—3219 (Clanwilliam): north facing gravelly slopes, Middelberg Pass near Kleinplaas, Citrusdal (—CA), 777 m (2 550 ft.), 12/7/1975, *Williams 2017* (NBG, holotype; BOL, K, M, MO, PRE, S, STE, isotypes).

Macrostylis ramulosa is distinct on account of being a semi-decumbent shrub with many branchlets sprouting towards the base, with linear-lanceolate or subulate, acute, pubescent leaves, hairy at the tips, without any prominent midrib, with pubescent bracts 2, 4–4, 5 mm long, with bracteoles and calyx pubescent at their tips, with the style simple and with the fruits pubescent. It differs from *M. villosa* (Thunb.) Sond. which has leaves rather flat and prominently keeled, not round backed, and from *M. decipiens* E. Mey. ex Sond. which is a much more glabrous plant with smaller leaves, with the apex often bi-glandular truncate not blunt and hairy.

4. *Macrostylis decipiens* E. Mey. ex Sonder in Flor. Cap. **1**: 439 (1860). Type: Rocky places at Piquetberg, 1 500–2 000 ft., (111, A, d, 23), 13/11/1828 *Drège s.n.* (S, lectotype; MEL, isotype).

Macrostylis decipiens E. Mey. in Drège, Zwei Pflanz. Doc.: 200 (1844) nom. nud. Type: as above.

Shrubs 200–300 mm tall, many-stemmed with a persistent root, coppicing after fires. *Branches* short, erect, slender, sparsely puberulous becoming glabrous, pale becoming reddish-brown, well-clothed with leaves. *Leaves* 4–6 mm long, 1, 4–1, 8 mm broad, lanceolate, acute, sessile, alternate, erect, imbricate; apex often truncate; margins ciliolate, gland-dotted; adaxial surface glabrous,

flat; abaxial surface sparsely puberulous or glabrescent, gland-dotted along the midrib. *Inflorescence* terminal, sessile, up to 8-aggregate. *Bract* one to each flower, outermost leaf-like, inner 1,2 mm long, 0,7 mm broad, lanceolate, puberulous, ciliolate. *Bracteoles* two, 0,8 mm long, 0,6 mm broad, ovate-lanceolate, puberulous, ciliolate. *Calyx lobes* five, 2 mm long, 1 mm broad, lanceolate, obtuse or trunculate, ciliolate; midrib sparsely pubescent above. *Petals* five, 5 mm long; *limb* 1,8 mm diam., approximately orbicular, white; *claw* 3,2 mm long, 1,1 mm broad, strongly bearded above with erect hairs, shorter crisped pubescent below, eciliate, narrowing and glabrous towards the base. *Staminodes* five, 0,05 mm long, vestigial, situated in a depression on the disc at the base of the petal. *Filaments* five, becoming 6 mm long, glabrous, protruding. *Anthers* five, before anthesis 1,3 mm long, 0,7 mm broad, reddened, apical gland minute. *Pollen* 51–55 μ long, 21–23 μ diam., oblong. *Disc* green, closes over the ovary, exudes nectar. *Stigma* 0,12 diam., a minute red dot, simple. *Style* becoming 6 mm long, terete, glabrous, scarcely narrowing below. *Ovary* tri-carpellate, 0,6 mm diam., glabrous. *Fruit* 1,2 or 3-carpellate; carpels 12–14 mm long, glabrous, reddened; horns 3–5 mm long, erect or slightly recurved. *Seed* 5 mm long with the white aril protruding another $\frac{1}{2}$ mm at the apex, 2 mm broad, black, matt.

In validating E. Meyer's manuscript name for this plant, *Macrostylis decipiens*, Sonder cites collections by both Drège and Zeyher. That of Drège has been chosen as the lectotype as it was a portion of this collection that was seen by Meyer. Unfortunately the actual specimen seen by Meyer was lost when his herbarium, housed at Berlin, was destroyed by fire during the war. The descrip-

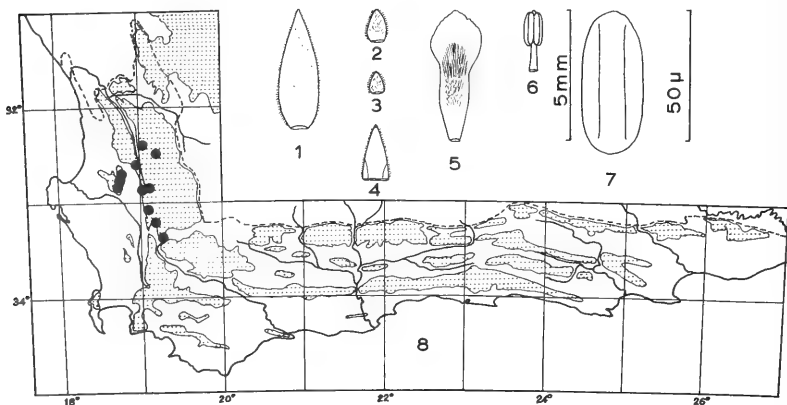


FIG. 4.

Macrostylis decipiens: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, pollen. 8, distribution.

tion given above, made from fresh material, amplifies that of Sonder in the *Flora Capensis*.

SPECIMENS EXAMINED

CAPE—3218 (Clanwilliam): In arenosis pr. Piqueniers kloof (—DB), 280 m, 22/8/1894, *Schlechter 4939* (BM, K, P, S, W, BR); W. slopes of Zebra Kop, Piketberg Mt., 3 000–3 500 ft., 23/5/1948, *Esterhuysen 14500* (BOL, K, LD, NBG); near The Rest, Olifants River Mtns., 25/9/1923, *Howes 180* (K, PRE, W); Zebra Kop, 3 500 ft., —/5/1948, *Stokoe s.n.* (SAM 64153), 900–2 900 ft., 14/10/1963, *Taylor 5339* (STE), 2 500–3 000 ft., 13/10/1963, *Esterhuysen 30401* (BOL); Piquetberg (—DC), 1 500–2 000 ft., 13/11/1828, *Drège 111. A. d.* (BM, BOL, E, G, K, LD, MEL, P 1884, PRE, S, SAM, W); plateau above Versveldts Pass, Piketberg Mt., 2 500 ft., 25/4/1948, *Esterhuysen 14474* (BOL, K, NBG); W. slopes of Levant, Piketberg Mt., 3 000 ft., 24/5/1948, *Esterhuysen 14505* (BOL, K, LD, NBG); Piketberg, 10/9/1950, *Maguire 431* (NBG), —/2/1940, *Zinn s.n.* (SAM); Vogelvley (—DD), 2 000 ft., 27/6/1896, *Schlechter 7921* (BM, BOL, E, G, GRA, K, P, PRE, S, W).

—3219 (Wupperthal): Lower N.E. slopes of Suurvleiberg (—AC), —/12/1939, *Esterhuysen 2490* (BOL); valley between Suurvleiberg and Vensterberg, 5 000 ft., —/12/1939, *Esterhuysen 2505* (BOL); S.W. slopes of Middelberg, —/12/1939, *Esterhuysen 2482* (BOL), 22/6/1942, *Esterhuysen 7855* (BOL), 25/9/1937, *Compton 7063* (NBG); Cedarberg, Algeria, N. slopes, 24/6/1942, *Esterhuysen 7844* (BOL), 1 400 ft., 23/1/1963, *Rycroft 2633* (NBG); Krom River Kloof, S. Cedarberg (—CA), 11/12/1950, *Esterhuysen 17970* (BOL); S.W. slopes of the Grootberg, 3 500 ft., 21/12/1940, *Esterhuysen 4151* (BOL, K); Grasruggens Mtns. (—CC), 26/11/1938, *Pillans 8787* (BOL); sandy vlakte, 24 Rivers Mtns., Porterville, 3 000 ft., 23/10/1949, *Esterhuysen 16145* (BOL, K, NBG), 10/10/1953, *Esterhuysen 21891* (BOL), 17/12/1962, *Esterhuysen 29959* (BOL); above Thee River and below Olifants River Dome, 11/5/1963, *Esterhuysen 30176* (BOL); Cardouw Pass, 4/11/1951, *Maguire 1219* (NBG); Berghof near Ratel River, Porterville Mtns., 2 600 ft., 27/9/1972, *Oliver 3923* (STE); Dasklip Pass summit, Cardouw Mtns., 2 400–2 600 ft., 6/10/1971, *Williams 1546* (NBG); Zuurvlaakte, Porterville Mtns., 3 400 ft., 24/1/1973, *Williams 1748* (NBG).

—3319 (Worcester): Inkruip. Witsenberg (—AA), 1/10/1954, *Esterhuysen 23484* (BOL); In montibus ad 24 Riveren, —/12/—, *Zeyher 293* (G, K, MEL, S, SAM); Mt. above Kliphuisvlakte, Porterville, 4 000 ft., 24/1/1973, *Williams 1753* (NBG); Mitchells Pass (—AD), 1 000 ft., 14/1/1897, *Schlechter 9951* (BM, BOL, G, GRA, K, P).

DISTRIBUTION AND VARIATION

Macrostylis decipiens is found growing in rather dry stony sand derived from the Table Mountain Sandstone at altitudes varying from 250 to 1 500 metres

above sea level. Populations extend from the vicinity of Mitchells Pass near Ceres in the south to the Krakadouwsberg near Clanwilliam in the north with outliers on the Piketberg to the west and on the Gifberg near Vanrhynsdorp in the north.

There appears to be considerable variation in the pubescence of this plant. A collection from near Algeria (Rycroft 2633) has branchlets and leaves completely glabrous and even glaucous with the leaves eciliate thus varying from the more normal condition where the branchlets and leaves may be sparsely puberulous and ciliolate or serrulate. A collection from Apollo Peak in the Southern Cedarberg (Esterhuysen 25515) shows leaves that are puberulous and considerably broader than usual.

Macrostylis decipiens from mountainous areas, appears to be most closely related to *M. villosa* which is found in the sandy plains. Both species frequently produce leaves in which the midrib and margins terminate at the apex in two separate points, giving a truncated appearance to the leaf. This is a valuable diagnostic character. The leaves of *Macrostylis decipiens* are however very much smaller. Another character which these two plants share is an ability to coppice from the rootstock after fires.

Furthermore, *M. decipiens* is distinct in having the stigma simple, and leaves lanceolate-acute with a distinct midrib usually 4 to 6 mm long. It differs from *M. villosa* which has leaves 4–13 mm long and from *M. ramulosa* which has leaves subulate, without a distinct midrib. *M. decipiens* can be distinguished from *M. tenuis* in that it is a plant with many erect stems that may coppice from the root after fires whereas *M. tenuis* is single-stemmed at base. The branchlets of *M. decipiens* tend to be erect, the leaves lanceolate and the fruit always 3-carpellate whereas in *M. tenuis* the branchlets may be spreading-erect, the leaves elliptic and the fruit two or three-carpellate.

5. *Macrostylis tenuis* E. Mey. ex Sonder in Flor. Cap. 1:440 (1860). Type: Rocky places on the Cedarberg, 3 000-4 000 ft., 13/12/1830 Drège *s.n.* (S, lectotype).

Macrostylis tenuis E. Mey in Drège Zwei Pflanz. Doc.:73,200 (1844) nom. nud. Type: as above.

Macrostylis ovata Sonder in Flor. Cap. 1:441 (1860). Type: In interioribus Prom. Bonae Spei, Niven *s.n.* (BR-MART 1150, S).

Shrubs 0,15 to 0,9 m tall, spreading up to 2 m, dense or diffuse, branching from ground level. *Branches* numerous, spreading-erect, glabrous; *bark* ashy-brown, fairly smooth. *Branchlets* numerous, spreading-erect, often dichotomous, fairly short, rigid, minutely puberulous. *Leaves* up to 3 mm long, 0,8–1,6 mm broad, ovate or elliptic, obtuse, rather thick or sometimes flat, sessile, spreading-erect, usually alternate, glabrous or puberulous on both sides, gland dots scattered; margins scabrid-denticulate, gland-dotted. *Inflorescence* terminal,

up to 6-aggregate; flowers 2.5 mm diam., crowded, sessile, white-cream coloured. *Bract* varies, 1.2–1.7 mm long, 0.6–1.2 mm broad, ovate, obtuse, puberulous, gland-dotted; margins scabrid-puberulous. *Bracteoles* two, 1 mm long, 0.4–0.6 mm broad, elliptic, obtuse, puberulous, ciliolate. *Calyx lobes* five, 1.3–1.5 mm long, 0.4–0.7 mm broad, oblong, obtuse, adaxially puberulous, gland-dotted, ciliolate. *Petals* five, 2.6 mm long overall; *limb* 0.9–1.1 mm broad, orbicular, gland-dotted; *claw* 1.5 mm long, narrowing to the base, densely crisped bearded above mostly towards the midrib. *Staminodes* five, 0.1 mm diam. or less, vestigial, at the base of the disc. *Filaments* five, becoming 3–4 mm long, filiform, glabrous. *Anthers* five, 0.7 mm long, 0.5 mm broad, reddened; apical gland globose, sessile. *Pollen* 45–51 μ long, 18–21 μ broad, oblong. *Disc* fleshy, green, closes over the ovary. *Stigma* 0.1 mm diam., red, simple. *Style* becoming 4–5 mm long, glabrous. *Ovary* 2 or 3-carpellate, 0.5 mm long, 0.3–0.5 mm broad, glabrous; apices setulose. *Fruit* 2 or 3-carpellate, 12 mm long including the horn about 4 mm long, carpels smooth or puberulous, gland-dotted, reddened, only one or two may develop. *Seed* 5.2 mm long, with the white aril projecting a further 1–2 mm, 2.2 mm broad, black, mottled, matt.

Specimens distributed by Drège labeled "*Macrostylis tenuis* E.M." appear to have been part of a mixed collection. The name *Macrostylis tenuis* validated by Sonder applies to one of the elements in this collection. The other element, which Sonder probably never saw is a plant belonging to the species *Macrostylis*

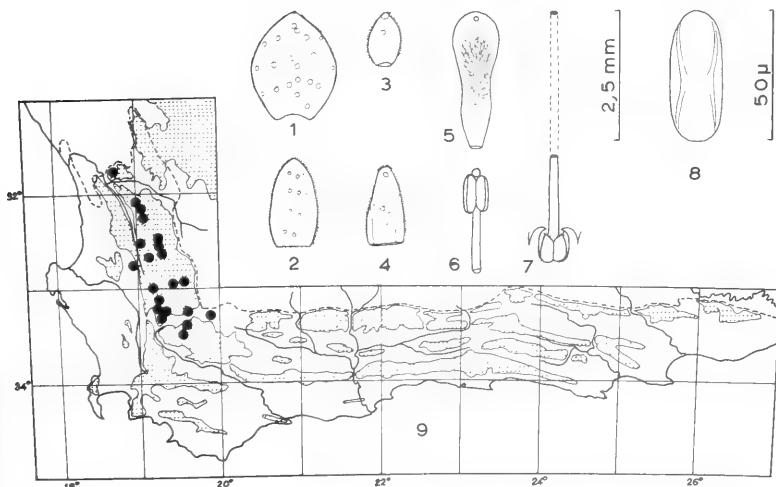


FIG. 5.

Macrostylis tenuis: (from Williams 2080) 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, gynoecium and disc. 8, pollen. 9, distribution.

squarrosa Bartl. & Wendl. *M. tenuis* has been collected many times and over a large geographical range by Miss E. Esterhuysen of the Bolus Herbarium. The above description made mainly from fresh material (Williams 2000, Williams 2080) amplifies that given by Sonder and describes the variation encountered in this species.

SPECIMENS EXAMINED

CAPE—3118 (Vanhynsdorp): Giftberg, Vanhynsdorp Division (–DC), 2 000 ft., 15/10/1953, *Esterhuysen* 22126 (BOL).

—3219 (Wupperthal): Pakhuis, Clanwilliam Division (–AA), 29/9/1940, *Esterhuysen* 3150 (BOL), 29/9/1940, *Esterhuysen* 3151 (BOL), above 3 500 ft., –/12/1940, *Leipoldt* 3348 (BOL, NBG), 28/12/1941, *Esterhuysen* 7389 (BOL), 20/9/1942, *Esterhuysen* 8011 (BOL), 17/1/1953, *Esterhuysen* 21156 (BOL); between Pakhuis and Heuningvlei, Cedarberg Mountains, Clanwilliam Division, 28/12/1941, *Esterhuysen* 7431 (BOL), 28/12/1941, *Esterhuysen* 7454 (BOL); Cedarberg, –/3/1932, *Stokoe* 2604 (BOL, SAM); Heuningvlei and on the Koudeberg, Cedarberg, 3 000–4 000 ft., 111.A.D.10, 13/12/1830, *Drège* s.n. (BM, MEL, S); Heuningvlei, 23/9/1942, *Esterhuysen* 8063 (BOL); between Heuningvlei and Haasvlei, 15/1/1953, *Esterhuysen* 21134 (BOL); between Heuningvlei and Koupoort (–AC), 2 000–3 000 ft., 21/10/1945, *Esterhuysen* 12114 (BOL); between Heuningvlei and Boontjieskloof, 31/12/1941, *Esterhuysen* 7522 (BOL); Krakadouw Peak, Cedarberg, –/12/1941, *Stokoe* s.n. (SAM 58849); between Crystal Pool and Scorpions Poort, 26/6/1942, *Esterhuysen* 7903 (BOL); shale band below Cedarberg Tafelberg, Clanwilliam Division, 5 000 ft., 16/12/1950, *Esterhuysen* 18161 (BOL); Welbedagt Kloof below Cedarberg Tafelberg, 26/9/1942, *Esterhuysen* 8106 (BOL); Dwarsrivier, sandy flats amongst rocks (–AD), –/3/1940, *Esterhuysen* 2511 (BOL); at foot of Wolfberg, Cedarberg, 26/12/1953, *Esterhuysen* 22471 (BOL); Krom River Kloof, S. Cedarberg, Clanwilliam Division (–CA), 3 000–4 000 ft., 11/12/1950, *Esterhuysen* 17991 (BOL); Apollo Peak, 3 000–4 000 ft., 31/3/1956, *Esterhuysen* 25515 (BOL); east spur of Hondverbrand Ridge, S. Cedarberg, Ceres Division, 21/4/1946, *Esterhuysen* 12737 (BOL); Duiwelskop, near Citrusdal, Clanwilliam Division, 3 500 ft., –/1/1945, *Stokoe* 9144 (BOL, SAM); Donkerkloof Kop, –/1/1945, *Stokoe* s.n. (SAM 58846); Cold Bokkeveld Mtns. at Elands-kloof, Clanwilliam Division, 25/3/1951, *Esterhuysen* 18453 (BOL); Gideonskop, S. Cedarberg, Ceres Division, 4 000 ft., 6/4/1947, *Esterhuysen* 13887 (BOL); Dwarsriviersberg, South Cedarberg, Clanwilliam Division (–CB), 3 500–4 000 ft., 1/4/1956, *Esterhuysen* 25554 (BOL); Krom River, S. Cedarberg, 3 000–4 000 ft., 4/10/1952, *Esterhuysen* 20492 (BOL); ridge S. of Krom River, S. Cedarberg, 3 500 ft., 18/9/1975, *Williams* 2085 (NBG); Onderboskloof, Ceres Division (–CC), 26/10/1966, *Esterhuysen* 31630 (BOL); sandy flats between 24 Rivers and Pikeniers Kloof, 400–800 ft., 111. D.a. 16/1/1831, *Drège* 7149 (G, P); Keerom, 3/12/1950,

Esterhuysen 17870 (BOL); Schurweberg Peak, N.E. of Bokkeveld Tafelberg, Ceres Division (-CD), 31/12/1961, *Esterhuysen* 29430 (BOL), 1/12/1962, *Esterhuysen* 29449 (BOL); Stompiesfontein, Swartruggens, Ceres Division (-DC), 3 500 ft., 18/11/1961, *Esterhuysen* 29333 (BOL); Groenfontein, Swartruggens, 4 000 ft., 20/11/1974, *Williams* 1930 (NBG), 3 900 ft., 18/9/1975, *Williams* 2080 (NBG).

—3319 (Worcester): Boboskloof, ridge S. of ruin (-AA), 720–1060 m, 22/11/1975, *Williams* 2151 (NBG); Visgat, upper Olifants River Valley, Ceres Division, 26/12/1946, *Esterhuysen* 13405 (BOL, K, NBG, P); Visgat, 15 miles N. of Die Vlakke, 2 000 ft., 30/12/1962, *Taylor* 4545 (PRE, STE); Visgat, Ceres Division, 820 m, 15/5/1975, *Williams* 2000 (NBG), 620 m, 2/12/1975, *Williams* 2155 (NBG); Witsenberg Vlakke a few miles before Visgat, 2 000–3 000 ft., 11/1/1960, *Esterhuysen* 28401 (BOL); Rocklands Peak, Cold Bokkeveld, Ceres Division, 4 500–5 000 ft., 5/6/1955, *Esterhuysen* 24326 (BOL); Koude Bokkeveld, Skurfdebergen pone Elandsfontein, Ceres Division, 5 500 ft., 18/1/1897, *Schlechter* 10040 (BOL, BR, E, G, GRA, K, P, W); Hansiesberg, W. slopes, Ceres Division, 4 000–5 000 ft., 18/4/1956, *Esterhuysen* 25706 (BOL); Gydoberg, N. Slope, 10/11/1946, *Walgate* 1117 (BOL); Baviaansberg, Ceres Division (-BA), 5 500 ft., 4/11/1962, *Esterhuysen* 29803 (BOL), -1/1937, *Stokoe* 4549 (BOL); Baviaansberg slopes above Karroo Poort, 30/6/1940, *Esterhuysen* 2578 (BOL); Koedoedouw Kloof, Ceres Division (-AD), 31/1/1954, *Esterhuysen* 22550 (BOL, K); Valschgat Kloof, Roodeberg, Ceres Division (-BC), 4 000 ft., -1/1940, *Esterhuysen* 1543 (BOL); Roodeberg, 6 000 ft., -12/1940, *Stokoe* 7667 (BOL), 5 000 ft., 19/1/1940, *Compton* 8407 (NBG), 27/12/1952, *Esterhuysen* 20910 (BOL); Matroosberg, shale band on plateau near Peak "C", 5 000 ft., -1/1941, *Stokoe* s.n. (BOL, SAM 58813); sandy flats at N.E. foot of Matroosberg, 6/8/1951, *Esterhuysen* 18741 (BOL); Matroosberg near Laakenvlei Kloof, 3 500 ft., 20/1/1917, *Phillips* 1960 (SAM); In convalle Hex River prope De Doorns, Worcester Division, -1/1908, *H. Bolus* 13080 (BOL, BM, K, GRA, STE); foot of Kvados Mtns. near Orchard, 24/11/1944, *Esterhuysen* 10932 (BOL); Bokkerivier Farms, 19/3/1974, *Thompson* 4 (NBG); Bonteberg, Eikenboschhoek, 3 500–4 000 ft., 3/11/1940, *Esterhuysen* 3652 (BOL); 2,7 km beyond Sandhills turnoff, Worcester Division (-DA), 1 550 ft., 4/12/1971, *Williams* 1606 (NBG); Buffelshoekkloof, 28/4/1942, *Esterhuysen* 7811 (BOL); Blaaskloof, at W. base of Keeromsberg, 23/2/1958, *Esterhuysen* 27585 (BOL); sandy rocky slopes above Sandhills, Hex River Valley, Worcester Division, 28/9/1978, *Esterhuysen* 35048a (BOL).

DISTRIBUTION AND VARIATION

Macrostylis tenuis is found growing in stony or hard sandy ground associated with the Table Mountain Sandstone at altitudes varying from about 200 to 1 800 metres above sea level. The geographical distribution extends in a more or less

north-south direction from the Giftberg near Vanrhynsdorp to near Sandhills in the Hex River Valley, a distance of approximately 210 km. Over this range of distance and altitude there is some variation in the species. In only one case (*Esterhuysen 21156*) has it been noted that leaves which are normally alternate, may be found to be opposite. Without apparent reason leaves may be glabrous, scabrid, clothed with a short spiky pubescence or quite hairy. Although in most cases the leaves are spreading-erect, they may also be found to be adpressed (*Esterhuysen 17991*) or spreading (*Esterhuysen 22550*). Fruits usually have very long horns. The longest are on specimens from the Giftberg (7 mm, *Esterhuysen 22126*) at the northern limit of distribution and the shortest on specimens from the Hex River Valley (1.5 mm, *Bolus 13080*) at the southern limit of distribution.

Macrostylis tenuis is recognised as distinct being a shrub arising from a single stem at ground level, not coppicing after fires, having branchlets spreading-erect, leaves elliptic or ovate, obtuse with gland dots scattered and on margins, with the apex thickened, the style simple and fruits 2 or 3-carpellate. It differs from *M. decipiens* which coppices after fires, has erect branchlets, lanceolate leaves and fruits always 3-carpellate. It differs from *M. cauliflora* which has a capitellate style.

6. *Macrostylis cauliflora* Williams in Jl S. Afr. Bot. **41**(3): 183(1975). Type: CAPE—3419 (Caledon): near the Kouderivier between Gansbaai and Napier, Bredasdorp Division (—DA), 76 m alt., 27/2/1974, *Williams 1876* (NBG, holotype; BOL, K, MO, M, PRE, STE, isotypes).

ADDITIONAL SPECIMEN EXAMINED

CAPE—3419 (Caledon): Kleinberg, Napier commonage, Bredasdorp Division (—BD), 240 m alt., 9/5/1978, *Williams 2492* (NBG).

Macrostylis cauliflora is recognised as distinct being a small shrub with leaves gland-dotted only on the midrib and margins, and with the stigma capitellate, rather larger than usual. It is in appearance most like *Macrostylis crassifolia* Sond. but differs in that the leaves of *M. crassifolia* are gland-dotted all over, not only on the midrib and margins.

7. *Macrostylis squarrosa* Bartl. & Wendl., Diosmeae in Beitr. Bot. **1**: 198 (1824). Type: Cap. b. Spei, in regione Olofrivier, *Hesse s.n.* (GOET—WENDL, lectotype; GOET, S, isotypes).

Macrostylis obtusa Bartl. & Wendl., Diosmeae in Beitr. Bot. **1**: 197 (1824). Type: Cap. b. Spei, pr. Olofrivier, *Hesse s.n.* (GOET, MEL, S).

Diosma squarrosa Wendl. nom. nud.

Diosma obtusa G. F. W. Meyer nom. nud.

Shrubs about 0,3 m tall, densely bushy, single-stemmed at base. *Branchlets* very short, erect or sub-erect, numerous, interlocking, somewhat reddish, puberulous at first, not hidden by the leaves. *Leaves* 3,3 mm long, 1,7 mm broad, smaller on branchlets, ovate or ovate-oblong, obtuse, sessile, alternate, spreading and strongly recurved; adaxial surface hollowed along the middle, glabrous except just at the base; abaxial surface with the prominent midrib gland-dotted and bristly with very short hairs; margins gland-dotted, thick, and bristly with scattered hairs. *Inflorescence* terminal; flowers 5 to 7-aggregate, sessile; petals white. *Bract* 2 mm long, 1 mm broad, leaf-like, the inner becoming much reduced. *Bracteoles* two, 0,9–1,1 mm long, 0,6–0,8 mm broad, ovate, translucent, pubescent, minutely ciliate. *Calyx lobes* five, 1,2 mm long, 0,4 mm broad, oblong, virtually glabrous; apex thick, obtuse; midrib prominent, gland-dotted, margins ciliate, translucent below. *Petals* five, 2,8 mm long overall; *limb* 1 mm broad, orbicular; *claw* 0,7 mm broad narrowing below, bearded and ciliate above. *Staminodes* 0,2 mm long, clavate, between petal and disc. *Filaments* five, becoming 5 mm long, acicular, glabrous. *Anthers* five, 0,8 mm long, 0,6 mm broad, yellowish; apical gland minute. *Pollen* 44 μ long, 21 μ diam., oblong. *Disc* closes over the ovary, smooth, dark green, exudes nectar. *Stigma* simple. *Style* becoming 5 mm long, filiform, glabrous. *Ovary* 3-carpellate, 0,5 mm diam., glabrous. *Fruit* 3-carpellate of which often only one matures, 9,5 mm long overall including the horn 3–4 mm long, 2,5 mm diam., glabrous except for a very few short bristles on the horn, conspicuously gland-dotted. *Seed* 4,8 mm long, 1,6–1,8 mm diam., black, mottled, matt; endosperm white on a truncated surface.

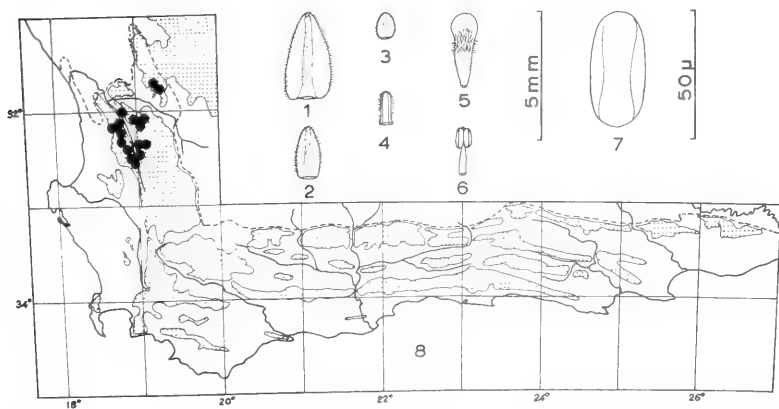


FIG. 6.

Macrostylis squarrosa: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, pollen. 8, distribution.

Macrostylis squarrosa appears to have been first collected by Hesse in the vicinity of the Olifants river (of which the name Olofrivier appears to be a corruption). Fragments of what were probably portions of the same collection were given the manuscript names of *Diosma squarrosa* by Wendland and *Diosma obtusa* B. & W. to synonymy. The above description based upon fresh material maintained the name *obtusa* as their *Macrostylis obtusa* but later Sonder, realising these taxa to be conspecific, upheld *M. squarrosa* B. & W. and reduced *M. obtusa* B. & W. to synonymy. The above description based upon fresh material (Williams 1759) supplements that previously given by Bartling & Wendland.

SPECIMENS EXAMINED

CAPE—3119 (Calvinia): Lokenberg, 21 miles S. of Nieuwoudtville, Calvinia Division (—CA), 13/10/1953, *Story* 4347 (GRA, K, PRE), 2 300 ft., 29/8/1953, *Acocks* 17041 (K, PRE); top of Botterkloof Pass, Calvinia Division (—CD), 24/8/1950, *Barker* 6514 (BOL, NBG).

—3218 (Wupperthal): \pm 1 mile N. of Seekoevlei (—BA), 1 250 ft., 22/8/1976, *Williams* 2192 (NBG); $\frac{3}{2}$ miles E. by N. of Graafwater, 1 100 ft., 22/8/1958, *Acocks* 19652 (PRE); Pakhuis Pass, Clanwilliam Division (—BB), —/8/1934, *Pillans* 7078 (BOL, PRE), 29/9/1940, *Esterhuysen* 3152 (BOL, SAM), 2 800 ft., 4/10/1897, *H. Bolus s.n.* (BOL), —/2/1941, *Leipoldt* 3662 (GRA, K, NBG), 7/12/1934, *Salter* 5035 (K), 2 500 ft., 2/10/1948, *Acocks* 15030 (K, PRE), 1/12/1934, *Compton* 4768 (NBG), 17/8/1939, *Compton* 7742 (NBG), 30/9/1940, *Compton* 9599 (NBG), 5/9/1948, *Compton* 20940 (NBG), 7/9/1949, *Barker* 5621 (NBG), 6/9/1951, *Johnson* 253 (NBG), 19/10/1965, *Barker* 10317 (NBG), 1 000–2 500 ft., 3/9/1947, *Story* 2972 (PRE), 9/9/1938, *Gillett* 4065 (BOL, PRE), 27/8/1937, *Compton* 6851 (NBG); Kransvlei, 14/9/1947, *Compton* 20030 (NBG); Nardouw kloof, —/9/1947, *Stokoe s.n.* (SAM 64156); 5 miles W. of Clanwilliam, —/7/1948, *Lewis s.n.* (SAM 64155); N. slope of the Schimmelberg, Clanwilliam Division (—BD), 12/10/1939, *Pillans* 9117 (BOL, GRA, K, NBG); Kransvallei/Elandsfontein, top of rise, —/9/1947, *L. Bolus s.n.* (BOL 23756); Lambertshoekberg, 10/9/1950, *Barker* 6706 (BOL, NBG), 31/8/1935, *Compton* 5559 (NBG); Haarwegskloof near Marcuskraal, 1050 ft., 1/12/1976, *Williams* 2251 (NBG); Blauwberg (N.E. of Citrusdal) Clanwilliam Division (—DB), 1 500 ft., 10/8/1896, *Schlechter* 8469 (BM, BOL, G, GRA, K, P, PRE, S, W); in arenosis pr. Piqueniers Kloof, 850 ft., 22/8/1894, *Schlechter* 4939 (BOL ex parte, GRA, MEL, PRE, STE).

—3219 (Clanwilliam): in fruticetis inter Pakhuis et Biedouw (—AA), 4/10/1897, *H. Bolus* 8956 (BOL); between Pakhuis and Heuningvlei, 28/12/1941, *Esterhuysen s.n.* (BOL); rocky places between Heuningvlei and Biedouw 2 500–3 000 ft., 13/12/1830, *Drège s.n.* (E, G, MEL, P 7156, S, W) part of a mixed collection; Pakhuis near village, 13/9/1947, *Barker* 4688 (NBG); Nieuwoudt Pass, Clanwilliam Division (—AC), 2 000 ft., 26/9/1934, *Leighton s.n.* (BOL

21582, P), 13/12/1941, *Compton* 12680 (NBG), 1 900 ft., 8/10/1975, *Williams* 2102 (NBG), 4/9/1938, *Halfstrom & Acocks* 790 (PRE, S); Cedarberg, Middleberg, S. slopes, 15/12/1941, *Esterhuysen* 7286 (BOL, NBG); Cedarberg, Middleberg, plateau, 14/12/1941, *Esterhuysen* 7209 (BOL), 11/2/1936, *Compton* 6250 (NBG); Algeria, Cedarberg, 16/12/1942, *Compton* 12768 (NBG); Algeria, bottom of Cedarberg Pass, 2 000 ft., 13/2/1973, *Williams* 1759 (NBG); between Alpha and Uitkyk Pass, Cedarberg, 26/9/1934, *Acocks* 3034 (S); Brakfontein, -/8/-, *Zeyher* 50 (S); in solo ericeto-arenosa (altit. 11,111) laterum montium prope Brakfontein, Clanwilliam Division, -/8/-, *Ecklon & Zeyher* (G, GOET, K, MEL, P, SAM, W).

DISTRIBUTION AND VARIATION

Macrostylis squarrosa is found growing in sandy ground derived from the surrounding Table Mountain Sandstone at heights varying from 260 to 850 m above sea level on the mountains flanking the Olifants River in the Clanwilliam Division. The distribution extends from near Citrusdal in the south to Nardouwsklouf in the north, a distance of about 70 kilometres, with disjunct populations a further 45 kilometres away on the Bokkeveld mountains in the Calvinia Division.

There appears to be a certain amount of variation in the degree of pubescence on the leaves and fruits and also in the amount by which the leaves are recurved. The variation in these characters is however of no taxonomic significance.

Macrostylis squarrosa is distinct in having a densely bushy squarrose habit with the leaves ovate or oblongovate, obtuse, spreading and strongly recurved and in having the stigma simple.

8. *Macrostylis crassifolia* Sonder in Flor. Cap. 1: 440 (1860). Type: Bergvallei, Clanwilliam Division, -/1/- *Zeyher* 294 (S, lectotype; BM, BOL, G, GOET-WENDL, K, LD, MEL, P, PRE, SAM, W, isotypes).

Macrostylis crassifolia Sond. var *affinis* Sond. in Flor. Cap. 1: 440 (1860). Type: *Drège* 7157 (S, lectotype; K, P, W, isotypes).

Shrubs 1 m tall, round, dense with many stems arising from ground level. *Branches* numerous, fairly erect, glabrous; bark rough, dusky-brown. *Branchlets* numerous, slender, erect, very sparsely puberulous, not hidden by the leaves. *Leaves* 2–3.6 mm long, 1.5–2.0 mm broad, elliptic, obtuse, sessile, glabrous, subglaucous, spreading-erect, alternate; abaxial surface gland-dotted all over, midrib prominent; margins thick, gland-dotted. *Inflorescence* terminal with flowers creamy-white, sessile, up to 8-aggregate. *Bract* one to each flower, 0.8–1.4 mm diam., the outermost larger, orbicular, obtuse, glabrous, gland-dotted. *Bracteoles* two, 1 mm long, 0.6 mm broad, asymmetrically orbicular, ciliate, glabrous, gland-dotted. *Calyx lobes* five, 1.5 mm long, 0.8 mm broad, oblong,

very obtuse, apex thickened, glabrous, gland-dotted; margins below translucent and ciliolate. *Petals* five, 3 mm long over all, creamy-white; *limb* 1,2 mm broad orbicular; *claw* 1,1 mm broad, narrowing to the base, strongly crisped bearded and ciliate. *Staminodes* completely absent. *Filaments* five, becoming 6 mm long, acicular, glabrous. *Anthers* five, before anthesis 1,2 mm long, 0,6 mm broad, cream-coloured, pinkish above; apical gland minute, globose. *Pollen* 45 μ long, 23 μ broad, oblong. *Disc* closes right over the ovary, dark green, excudes nectar. *Stigma* simple, a red dot at the apex of the style. *Style* becoming 6,6 mm long, terete, glabrous. *Ovary* tri-carpellate, 0,5 mm long, 0,6 mm diam., glabrous. *Fruit* normally 3-carpellate (in a random sample of 87 fruits, 6 had 4 carpels. Of the remaining 3-carpellate fruits, 13 developed all three carpels, 35 developed only two and 33 developed only one carpel) 12,5 mm long overall, glabrous, gland-dotted; *horns* about 4 mm long, spreading at 45°, apex emarginate. *Seed* 6,3 mm long overall including the white aril, 2,1 mm broad, black, matt, mottled.

The type material of *Macrostylis crassifolia* was collected by Carl Zeyher in January (the actual year remains a mystery) on the farm Bergvallei, then belonging to Jacob Engelbrecht, in the Clanwilliam District. Duplicates were subsequently distributed to many herbaria. In the case of Sonder's herbarium, which is now divided between Stockholm and Melbourne, duplicates can be found in both herbaria. Of these, that preserved in Stockholm has been chosen as the lectotype. The specimen Drège 7157, without locality, which is the type of Sonder's var. *affinis*, is considered to be conspecific with *Macrostylis crassifolia*.

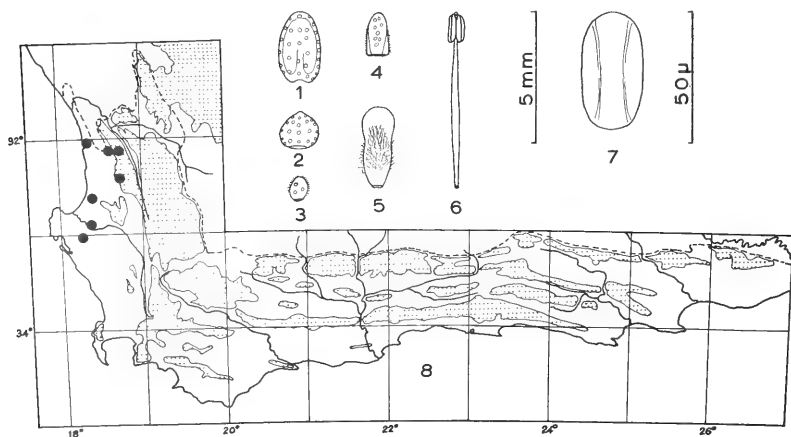


FIG. 7.

Macrostylis crassifolia: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, anther. 7, pollen. 8, distribution.

The above description made from fresh material supplements that of Sonder in the *Flora Capensis*.

SPECIMENS EXAMINED

CAPE — 3218 (Clanwilliam): Nortier Reserve, Lamberts Bay (—AB), —/1/1947, *Leipoldt* 4330 (BOL); 3.5 miles E. by N. of Graafwater, Clanwilliam Division (—BA), 1 100 ft., 22/8/1958, *Acocks* 19652 (K); Zeekoevlei (—BA/BB), 24/7/1941, *Esterhuysen* 5614 (BOL); 15 km from Clanwilliam on the Lamberts Bay road, 1 100 ft., 15/8/1973, *Williams* 1851 (NBG), 1852 (NBG); Clanwilliam (—BB), 20/7/1941, *Esterhuysen* 5608 (BOL); Bergvallei, Clanwilliam Division (—BC), —/1/—, *Zeyher* 294 (BM, BOL, G, GOET-WENDL, K, LD, MEL, P, PRE, S, SAM, W); between Bergvallei and Langevallei at Zwartbastkraal, 500–1 000 ft., 19/11/1828, *Drège* 7154b (G, LD, MEL, P, S); sandy heights at Bergvallei, 500 ft., 9/7/1830, *Drège* 7154a (K, P, W); 4 miles N. of Papkuilsfontein near Aurora, Piketberg Division (—CB), 250 ft., 16/11/1977, *Williams* 2392 (NBG); Piketberg, sandy plains and river, *Niven* 32 (BM); Rhasgat on the Berg River near Kersfontein, Piketberg Division (—CD), —/1/1886, *Bachmann* s.n. (BOL).

— 3318 (Cape Town): 8 miles from Hopefield towards Langebaanweg (—AA), 250 ft., 29/3/1974, *Williams* 1882 (NBG); Hopefield (—AB), —/9/1905, *H. Bolus* s.n. (BOL), 10/12/1946, *Leighton* 2457 (BOL), *Compton* 18925 (BOL, NBG).

Without locality: *Masson* s.n. (BM), *Zeyher* 289 (K, SAM), *Drège* 7157 (K, P, S, W), *Drège* s.n. (MEL, S).

DISTRIBUTION

Macrostylis crassifolia is found growing in dry sandy ground derived from the Table Mountain Sandstone at altitudes of from 30 to 330 metres above sea level, on the coastal plains from near Hopefield in the south to near Graafwater in the north, a distance of about 110 kilometres.

Macrostylis crassifolia is recognised as distinct being a dense shrub 1 m tall with leaves ovate, sessile, gland-dotted all over, with thick margins and thickened at the base.

9. *Macrostylis hirta* E. Mey. ex Sonder in Flor. Cap. 1: 441 (1860). Type: between Bergvallei and Langevallei (at Zwartbastkraal), Clanwilliam Division, 1 000 to 1 500 ft., 19/11/1828, *Drège* s.n. (S, lectotype; MEL, isotype; BM, E, G, K, P, PRE, W, duplicates).

Macrostylis hirta E. Mey. in *Drège* Zwei Pflanc. Doc.: 109, 200 (1844) nom. nud. Type: as above.

Macrostylis hirta E. Mey. var. *glabrata* Sond. loc. sit. Type: as above (MEL, S).

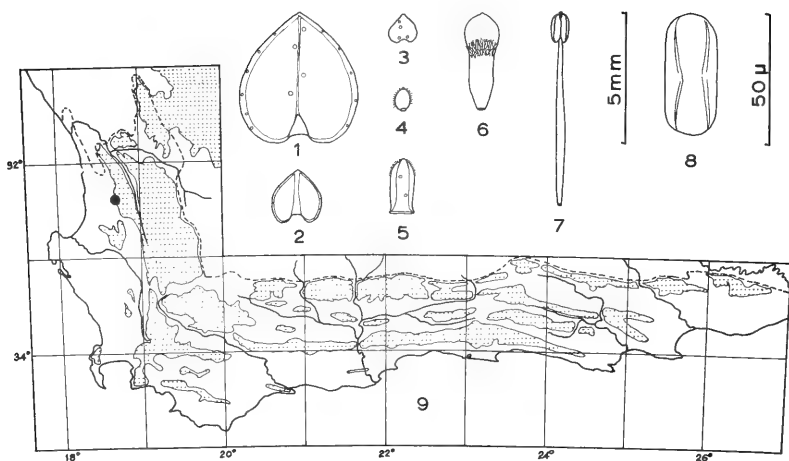


FIG. 8.

Macrostylis hirta: 1, large leaf. 2, small leaf. 3, bract. 4, bracteole. 5, calyx lobe. 6, petal. 7, anther. 8, pollen. 9, distribution.

Macrostylis wallichiana Dümmer in Fedde Repert. **11**: 120 (1912). Type: South Africa, Wallich s.n. (K, lectotype; G, BM, isotypes).

Shrubs up to 0,9 m tall or grazed down to 0,1 m, dense, with many stems arising from ground level. *Branches* glabrous, on vigorous young plants straight, erect and quite long but more usually short, spreading at 45° angles, interlocking. *Branchlets* slender, short, glabrous, spreading at 45°. *Leaves* on vigorous young plants 5 mm long, 4,2 mm broad, on older plants about 2,1 mm long, about 1,9 mm broad, ovate-cordate, sub-acute, sessile, alternate, glabrous, glaucous, flat, fleshy, spreading at 90°, margins eciliate, narrowly cartilagenous, somewhat thick; gland dots few on margins and midrib. *Inflorescence* terminal with flowers sessile, creamy-white, aggregated into groups of up to 7. *Bract* varies, outermost leaf-like, inner 1 mm long, 0,6–1,0 mm broad, sub-orbicular, glabrous, very sparsely ciliate, apex with a blunt point. *Bracteoles* two, 0,8 mm long, 0,6 mm broad, asymmetrically oblong; apex thick with a small obtuse point; midrib thickened; hyaline margins sparsely ciliate. *Calyx lobes* five, 2 mm long, 0,9 mm broad, oblong, obtuse with a small blunt point; margins broadly translucent, minutely ciliate above; adaxial surface minutely pubescent towards the apex; abaxial surface round, keeled, glabrous, obscurely gland-dotted. *Petals* five, 3,7 mm long overall; *limb* 1,7 mm broad, orbicular, obtuse. *Claw* 1 mm broad, very strongly crisped bearded above. *Staminodes* absent. *Filaments* five, becoming 6,3 mm long, straight, glabrous. *Anthers* five, before anthesis 1,1

mm long, 0.7 mm broad, wine-coloured; apical gland minute. *Pollen* 45 μ long, 20 μ diam., oblong. *Disc* green, curls over the ovary, exudes nectar. *Stigma* simple. *Style* becoming 7.5 mm long, straight, terete, glabrous, narrower below. *Ovary* 3-carpellate, 0.6 mm diam., glabrous. *Fruit* 3-carpellate, usually with one developing to maturity, 9.5 mm long overall, glabrous, gland-dotted, sometimes reddened; horn 3 mm long, fairly erect, apex bifid. *Seed* 5.5 mm long, including the aril 1 mm long, 1.8 mm broad, black, matt, mottled; aril white.

Drège collected this species on the 19th November 1828, according to a fully labelled specimen preserved in Paris, on the farm Swartbaskraal in the Clanwilliam Division. Sonder recognised that some plants may be more glabrous than others by proposing the variety *glabrata* at the same time as he validated E. Meyer's manuscript name *hirta*. Later Dümmer proposed the name *M. wallichiana* based on a rather glabrous specimen collected by Wallich at the Cape. This variation in pubescence not being thought to be a character worthy of recognition, *M. hirta* var. *glabrata* and *M. wallichiana* are both considered to be conspecific with *M. hirta* E. Mey. ex Sond. The above description of the glabrous form made from fresh material (Williams 1849) amplifies that of Sonder in the *Flora Capensis* (1860).

SPECIMENS EXAMINED

CAPE—3218 (Clanwilliam): between Bergvallei and Langevalei (at Zwartbaskraal), Clanwilliam Division (–BC), 1 000–1 500 ft. (111, E, a, 12), 19/11/1828, Drège s.n. (MEL, S, BM, E, G, K, P 1879, PRE, W); south end of Boekenberg, Swartbaskraal, 1 400 ft., 15/8/1973, Williams 1849 (NBG); 2 km south of Bo-Swartberg on road from Bergvalley (–BD), 1 700 ft., 11/7/1975, Williams 2013 (NBG).

Without locality: Cap. B. Spei., Wallich s.n. (K, G, S).

Macrostylis hirta is recognised as distinct having leaves ovate, cordate, sub-acute, spreading at right angles to the stem, fairly flat and not recurved as in *M. squarrosa* and in having the stigma simple, the calyx 2.5 mm long with the lobes glabrous.

10. *Macrostylis barbiger* (Linn. F.) Bartl. & Wendl. Diosmeae in Beitr. Bot. 1: 195 (1824).

Diosma barbiger Linn. f. Suppl. Plant.: 155 (1781). Type: Swartland, Thunberg s.n. (LINN 270/19, holotype; C, S, UPS–THUNB 5659, isotypes)

Shrubs about 0.3 m tall, fairly erect, diffuse, single-stemmed at base. *Bran-ches* short, flexuous, 2–3-chotomous, glabrous, brownish, rough with leaf scars. *Branchlets* short, slender, glabrous, yellowish, opposite, spreading or sub-erect, well-clothed with leaves. *Leaves* 6–12 mm long, 4–6.5 mm broad, ovate-cordate, acute, cuspidate, sessile, glabrous, opposite, spreading, pale green

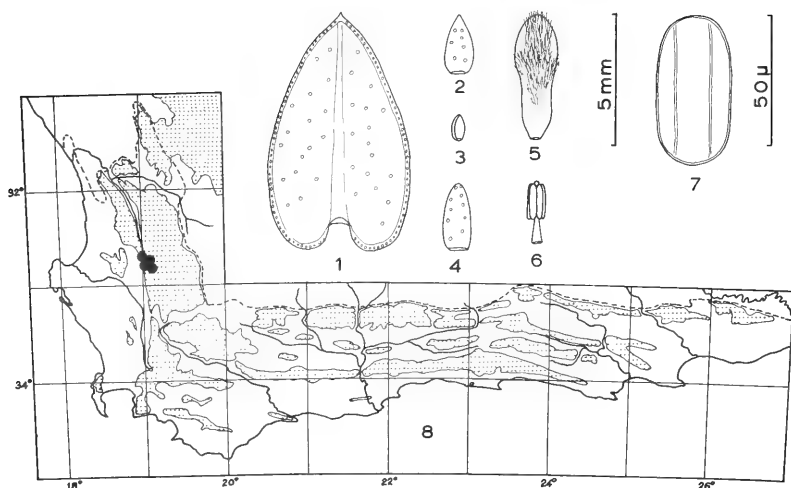


FIG. 9.

Macrostylis barbiger: 1, leaf. 2, bract. 3, bracteole (side view). 4, calyx lobe. 5, petal. 6, anther. 7, pollen. 8, distribution.

above, gland-dotted, glaucous and one-nerved beneath; margins narrowly cartilagenous, minutely gland-dotted. *Inflorescence* terminal, umbellate, in groups of up to 8 arranged in 4 opposite pairs, pendulous with the common peduncle 3–4 mm long deflexed; flowers pedicellate, white. *Bracts* one per floret, the outermost pair 2,2 mm long, 1,1 mm broad, the innermost about 1 mm long, lanceolate, glabrous, glaucous, gland-dotted. *Bracteoles* two, 1–1,3 mm long, oblong, complicate, glabrous at base of pedicel. *Pedicel* about 3,5 mm long, narrowing to the base, white, glabrous. *Calyx lobes* five, 2,5 mm long, 1,1 mm broad, oblong, obtuse, glabrous, gland-dotted, whitish. *Petals* five, 4,7 mm long overall, eciliate, densely bearded with shaggy hairs mainly on the midrib about the middle, the hairs projecting upwards from the throat of the flower; *limb* 1,7 mm broad, ovate; *claw* 1,1 mm broad. *Staminodes* vestigial, a minute gland 0,05 mm diam. at the apex of a filament 0,2 mm long. *Filaments* five, becoming 7,5 mm long, glabrous, terete. *Anthers* five, 1,3 mm long, 0,7 mm broad, orange-coloured; apical gland 0,15 mm diam., globose. *Pollen* 58 μ long, 28 μ diam., oblong. *Disc* closes over the ovary at first, dark green, exudes nectar. *Stigma* 0,3 mm diam., obtuse. *Style* becoming 9 mm long, terete, glabrous, very slightly narrower below. *Ovary* 3-carpellate, 0,7 mm diam., glabrous. *Fruit* 3-carpellate, of which one, two or three may develop, pedicellate, style persisting; *carpel* 10–12 mm long overall, glabrous, green; *horn* 3 mm long, erect, incurved. *Seed*

6.4 mm long (7.6 mm long overall including the white aril), 2.5 mm broad, black, matt, mottled.

In September 1773 C. P. Thunberg, accompanied by Francis Masson, traversed the Cardouw Pass across the mountains which divide the Swartland from the Olifants River Valley. There can be no doubt that it was here that he collected the type material of *Macrostylis barbiger*; it was here also that Zeyher made his collection of this species that was distributed to many herbaria. The above description, made from fresh material, supplements those of previous authors.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): slopes of Olifants River Mtns. near Warmbaths, Clanwilliam Division (—CA), 25/9/1911, *Stephens 7115* (BOL, GRA, K), *Stephens 7118* (BM, GRA, K), *Pearson 7115* (SAM), 2 000 ft., 8/7/1935, *Compton 5370* (BOL, NBG); Swartland (—CC), *Thunberg s.n.* (LINN 270.19, C, S, UPS—THUNB. 5659); in monte Kardouw, 1 500–2 000 ft., —/12/—, *Zeyher 295* (BM, C, E, G, GRA, K, MEL, P, PRE, S, SAM, W), *Hesse s.n.* (GOET); Cardouw Pass, Clanwilliam Division, 4/11/1951, *Maguire 1212* (NBG); Dasklip Pass near summit E. side, 2 400–2 600 ft., 6/10/1971, *Williams 1547* (NBG), 2 150 ft., 24/1/1973, *Williams 1747* (NBG), 2 000 ft., 7/11/1974, *Williams 1915* (NBG); hills a mile S.E. of Keerom, Clanwilliam Division, 25/11/1938, *Pillans 8705* (BOL, K); W. slopes of Cold Bokkeveld Mtns. above Olifants River Valley, 4/12/1950, *Esterhuysen 17923* (BOL); W. slopes below Olifants River Dome, 3 000 ft., 16/4/1949, *Esterhuysen 15307* (BOL); Onderboskloof, rocky slopes in upper Olifants River Valley, Ceres Division, 25/12/1947, *Esterhuysen 14311* (BOL, BM); Porterville, Piketberg Division, —/12/1956, *Loubser 808* (BOL).

Without locality: *Scholl 1118* (W), *Scholl 426* (W), *Edwards 6474* (SAM), *Edwards 262* (BOL), *Millar s.n.* (BM), *Masson s.n.* (BM), *Banks s.n.* (C), *Herb. Burmann s.n.* (G).

DISTRIBUTION

Macrostylis barbiger is not a rare plant and yet it has a strictly limited distribution being confined to the mountains on either side of the upper Olifants River, at heights lying between 600 and 900 metres above sea level. Its known range is about 12 km from east to west by about 20 km from north to south. The plants grow on dry, hard, stony or rocky ground derived from the Table Mountain Sandstone.

Macrostylis barbiger is recognised as distinct being completely glabrous with large ovate-cordate opposite leaves and with pendulous, umbellate flowers.

PUTATIVE HYBRIDS

M. barbiger is the only species in the genus possessing opposite leaves. Consequently, when a small population of *Macrostylis* plants with opposite leaves was discovered on the east side of Dasklip Pass it immediately excited attention. Unlike *M. Barbiger*, which has leaves cordate and glaucous, these specimens possessed leaves that are lanceolate and not at all glaucous.

There appears to be a distinct possibility that these plants are the result of hybridisation between *M. barbiger* and *M. decipiens* both of which occur in this area. Miss E. Esterhuysen has made a similar hybrid collection from Onderboskloof about 13 km to the east. In this case *M. barbiger* and *M. tenuis* are both found in the vicinity.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): East side of Dasklip Pass on road to Grootfontein, Clanwilliam Division (—CC), 2 200 ft., 23/9/1974, *Williams 1884* (NBG), 7/11/1974, *Williams 1914* (NBG); Onderboskloof, rocky slopes in upper Olifants River Valley, 2/1/1948, *Esterhuysen 14292 ex parte* (BOL).

SPECIES EXCLUDED

Macrostylis cordata G. Don Gen. Syst. 1: 789 (1831) = *Agathosma imbricata* Willd.

Macrostylis patersoniae Schonland in *Trans. R. Soc. S. Afr.* 1: 445 (1910) = *Acmaenia obtusata* (Thunb.) B. & W.

PHYTOGEOGRAPHY

Eight of the ten species of *Macrostylis* are found in the Clanwilliam Division. Of the remaining two, *M. villosa* is found on the Cape Peninsula, on the adjacent Cape Flats and on the West Coastal Plain while the other, *M. cauliflora*, is found in the Bredasdorp District—a disjunction of about 135 km to the east. Most species are found growing in sandy places amongst quartzitic rocks of the Table Mountain Geological Series. Three species *M. villosa*, *M. decipiens* and *M. crassifolia* appear to be able to withstand fires by coppicing from the root. Of these *M. villosa* and *M. crassifolia* are specially adapted to the sandy coastal plains having a very stout tap root penetrating deep into the sand. They appear to be unaffected by the moles which are abundant in these areas.

The one species with a large disjunction in its distribution pattern is *M. cassiopoides* where *M. cassiopoides* subsp. *dregeana* is found 112 km to the south of the nearest population of the typical subspecies. It is evident that these populations have been separated for long enough to be recognised at subspecific level. *M. tenuis* is a particularly variable species and also has the most widespread distribution both in altitude and distance. It is found as far north as the Giftberg

near Vanrhynsdorp and throughout the Cedarberg and Cold Bokkeveld mountains as far south as the Hex River Valley.

M. squarrosa shows a compact distribution in the vicinity of Clanwilliam with outliers on the Bokkeveld Mountains about 70 km away in the Calvinia Division.

Of fairly limited distribution are *M. ramulosa*, *M. cauliflora*, *M. hirta* and *M. barbiger*. *M. decipiens* is found on the mountains from Citrusdal to Ceres and on the Piketberg, an "island" of T.M.S. separated from the main north-south mountain ranges by a distance of 22 km. In this case one can only speculate that it must have been a very long time since these populations migrated to their present positions.

A FLORISTIC DESCRIPTION AND STRUCTURAL ANALYSIS OF THE PLANT COMMUNITIES OF THE PUNDA MILIA—PAFURI—WAMBIYA AREA IN THE KRUGER NATIONAL PARK, REPUBLIC OF SOUTH AFRICA:

2. THE SANDVELD COMMUNITIES

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ABSTRACT

The Sandveld communities of the Punda Milia-Pafuri-Wambya area in the Kruger National Park are described floristically and structurally. Habitat factors such as aspect, slope, soil, geology and altitude are discussed briefly. The floristic classification of the communities was done by means of the Braun-Blanquet method and the communities are described in terms of the most conspicuous as well as the differential species in the woody and herbaceous strata. The structural analysis was done by means of the Variable Quadrant Plot method and the discussion of the structure of the communities is based on the different growth forms, their canopy spread in different strata and the number of individuals per hectare.

UITTREKSEL

'N FLORISTIESE BESKRYWING EN STRUKTURELE ANALISE VAN DIE PLANTGEMEENSAPPE VAN DIE PUNDA MILIA-PAFURI-WAMBIYA-GEBIED IN DIE NASIONALE KRUGERWILDTUIN, REPUBLIEK VAN SUID-AFRIKA:

2. DIE SANDVELDGEMEENSAPPE

Die Sandveldgemeenskappe van die Punda Milia-Pafuri-Wambya-gebied in die Nasionale Krugerwildtuin, wat onderskeidelik deur middel van die Braun-Blanquetmetode en Varieerbare Kwadrantperseelmetode gemonster is, word aan die hand van hul floristiese samestelling en struktuur bespreek. Daar word kortliks na habitatkenmerke soos aspek, helling, grond, geologie en hoogte bo seespieël verwys. Die floristiese klassifisering van die verskillende gemeenskappe word aan die hand van die opvallendste en differensiërende spesies van die houtagtige en kruidagtige stratus beskryf. Die strukturele beskrywing is veral op die verskillende groeivorme, hul kroonverspreiding in verskillende stratus en die aantal individue per hektaar gegrond.

INTRODUCTION

The Punda Milia-Pafuri-Wambya area is situated in the northern part of the Kruger National Park and is bordered by Zimbabwe to the north and Mozambique to the east. The study area falls within the Transvaal Lowveld (L) climatic

*Based on an M.Sc. thesis, University of Pretoria.

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region of the South African Weather Bureau (Schulze, 1965) and according to the Köppen classification has a warm arid climate with a dry winter and a mean annual temperature exceeding 18 °C. The mean annual rainfall and temperature of Punda Milia and Pafuri are 549,1 mm; 22,9 °C and 415,2 mm; 24,2 °C respectively (Schulze, 1947; Weather Bureau, 1954, 1965; Reparticao tecnica de estatistica, 1961). In the preceeding paper (Van Rooyen, Theron and Grobbelaar, 1981a) environmental factors such as topography, drainage, geology, soils and climate were discussed in more detail.

To formulate a conservation and management policy, the emphasis must be on proper land use and for this purpose a classification of the vegetation is essential. Animal species differ in their habitat preferences and it is therefore important to locate the geographical distribution of these animal habitat types. Several factors determine the suitability of a habitat for a particular animal species, for example availability of food and visibility. Both these factors depend on floristic composition as well as vegetation structure. Relevant structural features include canopy regime and density of the various species at different height levels.

The objectives of this study were to classify the vegetation according to the Braun-Blanquet method (Werger, 1974) and to analyse the structure of the vegetation by the Variable Quadrant Plot method (Coetzee and Gertenbach, 1977).

METHODS

The Braun-Blanquet method, which was used in this study, is presently used in South Africa as basis for botanical surveys. The use of a uniform surveying method ensures comparable results and makes a hierarchical classification of the vegetation possible (Bredenkamp, 1975). This method has already been applied successfully on South African vegetation by Van Zinderen Bakker Jr. (1971); Coetzee (1972); Werger (1973); Bredenkamp (1975) and Boucher (1977) amongst others. The descriptive phrase included in the name of each community is based on the physiognomic vegetation classification of Tinley (1969).

For the structural analysis of the woody vegetation the Variable Quadrant Plot method was used (Van Rooyen *et al.*, 1981a). For each individual plant in the sample plot the species name, growth form, trunk diameter at ground level (if >100 mm), maximum height and the maximum canopy diameter in different strata were recorded. From the data the canopy spread and density of each plant species as well as each height class in the sample plot, were calculated. The canopy spread was expressed as a percentage of the sample plot area and density as number of individuals per hectare. The different strata that were investigated are: 0,5 m; 1 m; 2 m; 3 m; 4–5 m and >6 m (Van Rooyen *et al.*, 1981a). The height class to which an individual belongs corresponds to the stratum in which

the highest plant material of that individual occurs. The three growth forms which were distinguished are as follows:

- tree — individual with a single stem;
- sparse shrub — individual with two to four stems; and
- shrub — individual with more than four stems.

The field data were processed using computer programs. Tables were compiled for each sample plot and the mean values calculated for all the plots within a particular plant community. The following discussion is based on the latter values.

The total percentage canopy spread for a given stratum is obtained by

- (a) measuring the maximum canopy diameter of each specimen within that stratum on each sampling plot;
- (b) calculating a circular canopy cross-sectional area for each individual plant from the values referred to above;
- (c) calculating the sum of all the canopy cross-sectional areas of the given stratum referred to above for each sampling plot;
- (d) expressing each of the last mentioned figures as a percentage of the surface area of the relevant sampling plot; and
- (e) calculating the average value of the last mentioned values for the various sampling plots within a community.

The percentage apparent canopy cover (p.a.c.) is calculated as canopy cross-sectional area by using the largest canopy diameter measurement for each individual. The canopy cover for each group of individuals of the same species, growth form and height class is then calculated. This value is given as a percentage of the surface area of the sampling plot for the height class of that group. The total percentage canopy cover is then computed for each species and an average value of the latter values for the various sampling plots within a community is thus established.

RESULTS AND DISCUSSION

The classification of the vegetation in the study area stresses the correlation between habitat and floristic composition of communities as well as relationships between communities. Floristic composition and floristic relationship are shown in Table 1.

Differences and variations in the vegetation can often be ascribed to differences in geological formation, soil depth and rockiness of the soil surface, while climate, slope, pH of the soil, soil texture, soil structure, consistency and the concentration of salts in the soil all probably play a major role in the distribution of the plant communities.

The Sandveld communities are mainly found in areas underlain by Waterberg Sandstone, Cave Sandstone as well as the light red to white sands of the

TABLE 1

A constancy table of the plant communities of the Punda Milia—Pafuri—Wambiya area in the Kruger National Park*

PLANT SPECIES	COMMUNITIES																
	SANDVELD					COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
A <i>Burkea africana</i>	5																
<i>Fimbristylis hispidula</i>	3			1	1	1						1					
<i>Andropogon gayanus</i>	3					1						1					
<i>Holarrhena pubescens</i>	3																
<i>Bauhinia galpinii</i>	3				1												
<i>Ochna pulchra</i>	2		1														
B <i>Baphia massaiensis</i>		5															
<i>Grewia microthyrsa</i>		3															
<i>Combretum celastroides</i>		3				1											
<i>Hugonia orientalis</i>		3	1														
<i>Ptaeroxylon obliquum</i>		2															
<i>Pavetta catophylla</i>		2															
<i>Cleistanthus schlechteri</i>		2															
<i>Mariscus</i> sp.		2															
<i>Heinsia crinita</i>	1	2															
<i>Xylia torreana</i>		1															
C <i>Xeroderris stuhlmannii</i>			3														
<i>Aristida junciformis</i>	1		2														
<i>Aristida stipitata</i>	1		3	1													
<i>Indigofera inhambanensis</i>	1		2														
<i>Limeum dinteri</i>			2	1									2				
<i>Macrotyloma axillare</i>			2			1											
<i>Pavonia burchellii</i>			2									1					
<i>Balanites maughamii</i>		1	2		1								2				
D <i>Terminalia sericea</i>	3	2	5	4													
<i>Combretum collinum</i>	3	2	4	3	1								3				
<i>Tricholaena monachne</i>	2	2	3	1	1				1	1		1					
<i>Merremia tridentata</i>	4	3	3	3			1	1									
<i>Crotalaria sphaerocarpa</i>	1	1	2	3	1			1			1	1					
<i>Perotis patens</i>	3	3	3	3													
<i>Pteleopsis myrtifolia</i>	3	3	2	1	1												
<i>Eragrostis pallens</i>	2	4	2	2													
<i>Zygoon graveolens</i>	1	2	3	3			1										
<i>Aristida argentea</i>	2	2	1	1													

The constancy value of a plant species in a community is indicated by the following symbols: 1 (1–20 %); 2 (>20–40 %); 3 (>40–60 %); 4 (>60–80 %); 5 (>80–100 %)

*The complete differential table can be found in Van Rooyen (1978).

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Vitex amboniensis</i>	1	2	1	1		1						1					
<i>Vangueria infausta</i>	1	2	2	1													
<i>Siriga asiatica</i>	2	1		2													
<i>Xeromphis obovata</i>	1	1		2													
<i>Hippocratea crenata</i>		1		2	1												
<i>Acrotome inflata</i>				2													
<i>Blepharis subvolubilis</i>			1	2													
E <i>Kirkia acuminata</i>				1	1	5			2			1					
<i>Rhoicissus revoilii</i>		1			1	3											
<i>Croton gratissimus</i>		2				3											
<i>Azelia quanzensis</i>						3											
<i>Bridelia mollis</i>						2											
<i>Maytenus mossambicensis</i>	1				2												
<i>Indigofera lupatana</i>					1												
<i>Landolphia kirkii</i>					1												
<i>Asparagus falcatus</i>		1			1												
<i>Canthium huillense</i>					1												
<i>Rhus leptodictya</i>					1												
<i>Lagynias dryadum</i>					1												
<i>Elephantorrhiza burkei</i>					1								2				
<i>Brachylaena huillensis</i>					1												
F <i>Androstachys johnsonii</i>				1		5											
<i>Sporobolus panicoides</i>					1	4											
<i>Croton pseudopulchellus</i>	1				1	4											
<i>Commelina benghalensis</i>				1	1	3		1				1					
<i>Achyranthes sicala</i>						3											
<i>Setaria ustilata</i>						2											
<i>Leptocarydion vulpiastrum</i>				1		2											
<i>Cymbosetaria sagittifolia</i>						2		1									
<i>Selaginella dregei</i>						2											
<i>Panicum heterostachyum</i>						2											
<i>Barleria galpinii</i>						1											
<i>Panicum deustum</i>						1				1							
<i>Merremia pinnata</i>						1											
<i>Cyperus amabilis</i>		1				1											
G <i>Pellaea viridis</i>	2				3	2											
<i>Pellaea calomelanos</i>					2	2											
<i>Phyllanthus reticulatus</i>				1	2	2		1		1							
<i>Corchorus longipedunculatus</i>				1	1												
<i>Xerophyta retinervis</i>					1	1											
<i>Cleome monophylla</i>					1	1											
<i>Xerophyta equisetoides</i>					1	1											

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
H <i>Combretum zeyheri</i>	3	2	1	3	3	1											
<i>Borreria scabra</i>	1	2	3	1	1	2											
<i>Pogonarthria squarrosa</i>	4	2	2	3	2	1		1				2					
<i>Strychnos decussata</i>	1	2	1	1	1	1											
<i>Pseudolachnostylis maprounei</i> <i>folia</i>	5	1	1	2	2												
<i>Hexalobus monopetalus</i>	2	3	1	1	2												
<i>Strychnos madagascariensis</i> ..	3	2	4	3	3			1		3		1					
<i>Ipomoea magnusiana</i>	2	2	4	2		2	1	1				1					
<i>Guibourtia conjugata</i>	2	5	2		2												
<i>Rhynchosia resinosa</i>		2	3	1	2				1								
<i>Triumfetta pentandra</i>	1		1	2	1	2											
<i>Diplorhynchus condylocarpon</i> ..	4			1	3	1		1									
<i>Alchornea laxiflora</i>	1	4			2	1											
<i>Monodora junodii</i>	2	2		1	3	1											
<i>Celosia trigynia</i>	1	2			2	2		1									
<i>Waltheria indica</i>	2	2		2	3	1		1	1			2					
<i>Hymenocardia ulmoides</i>	2	2			3	1											
<i>Cassia absus</i>	1			2	1	1											
<i>Blepharis maderaspatensis</i> ..				1	2	2											
<i>Tephrosia elongata</i>	2	1	2	1	1			1									
<i>Rhynchosia venulosa</i>	1	1	2		1	1											
<i>Ariabotrys brachypetalus</i>	1	1	1	1	2						1						
<i>Agathisanthemum bojeri</i>	2	2		1	1			1									
<i>Tephrosia longipes</i>	2		1	1	1							1					
<i>Crabbea velutina</i>	1		2		1	1		1					2				
<i>Hippocratea longipedunculata</i> ..		1	1	1	1												
<i>Ximenia caffra</i>	1			1													
<i>Ozoroa paniculosa</i>	1			1	1						1						
<i>Ozoroa engleri</i>			1	1													
I <i>Urochloa mosambicensis</i>					1		5	1		1	1	2		4	2		
<i>Chloris virgata</i>					1		4	1	1					2			
<i>Acacia tortilis</i>							3	1								1	
<i>Salvadora angustifolia</i>									1								
<i>Boerhavia diffusa</i>							2										1
<i>Azima tetracantha</i>							2										
<i>Alternanthera pungens</i>							1										
<i>Trianthema triquetra</i>							1										
<i>Setaria verticillata</i>							1										
<i>Acacia senegal</i>					1		1										
<i>Cyathula crispula</i>							1										
J <i>Ximenia americana</i>			1	1			1	4									
<i>Enteropogon macrostachyus</i> ..					1	2	1	3	1								

PLANT SPECIES	COMMUNITIES																	
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4	
<i>Tetrapogon tenellus</i>							1	2										
<i>Chloris roxburghiana</i>							1	2										
<i>Acacia grandicornuta</i>							2	1										
<i>Amaranthus thunbergii</i>							1	1										
K <i>Commiphora glandulosa</i>					1		2	1	3		1							
<i>Abutilon fruticosum</i>					1	1	2	2	2									
<i>Ecobolium revolutum</i>							2	2	2									
<i>Sporobolus smutsii</i>	1			1	1		2	1	1									
<i>Thilachium africanum</i>				1			2	1	1				2					
<i>Corbichonia decumbens</i>							1	1	2									
<i>Sporobolus fimbriatus</i>								1	1									
<i>Aristida rhiniochloa</i>								1	1									
L <i>Enneapogon scoparius</i>										5								
<i>Euclea schimperii</i>				1						4								
M <i>Terminalia prunioides</i>							1	3	2	3								
<i>Maerua parvifolia</i>							3	3	2	1			2					
<i>Seddera capensis</i>				2	1		1	2	3	5	1	1						
<i>Elytraria acaulis</i>								2	2			1						
<i>Zanthoxylum capense</i>							1	1	2	2								
N <i>Themeda triandra</i>								1			5		2					
<i>Neorautanenien amboensis</i>								1	1		4							
<i>Setaria woodii</i>							1	1	1		3							
<i>Urochloa brachyura</i>								1			2							
<i>Panicum coloratum</i>											2		3					
O <i>Heteropogon contortus</i>	1				1		1	1	2	4	4	2	2	2				
<i>Bothriochloa insculpta</i>							1	2	3		4		2	2				
<i>Phyllanthus maderaspatensis</i> ..								1	2	2	1	1						
<i>Fingerhuthia africana</i>								1	2	3	1	2						
<i>Indigofera heterotricha</i>								1	2	1	2	1						
<i>Sorghum versicolor</i>								1	2		3	1						
<i>Heliotropium strigosum</i>				2					2		2	1						
<i>Oropetium capense</i>								1	1	1	1	1						
P <i>Colophospermum mopane</i>				2	1		3	5	5	5	5	5		5	4			
<i>Euclea divinorum</i>	1			1			1	3	1	2		1		5	3			
<i>Aristida congesta</i> subsp. <i>barbi-</i> <i>collis</i>				1			1	2	3	2	3	2						
<i>Neuracanthus africanus</i>					1		1	2	4	1	1	2						
<i>Barleria lancifolia</i>					1		1	2	2	2	2	1						
<i>Eragrostis rigidior</i>	1			1	1		1	1		2	2	1						

PLANT SPECIES	COMMUNITIES																	
	SANDVELD					COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS						
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1		2.2	3	4	1.1	1.2	1.3	1.4
<i>Eragrostis superba</i>							1	1	1	2	4	1						1
<i>Combretum hereroense</i>					1			1	1	1	1		3		2			1
<i>Dicoma tomentosa</i>								1	1	1		1	1					
<i>Dalechampia galpinii</i>									1	2								
<i>Aptosimum lineare</i>								1	2									
<i>Sterculia rogersii</i>					1				1	2		1						
Q <i>Combretum apiculatum</i>	2	2	5	4	5	1	1	1	5	4	2	5						
<i>Aristida congesta</i> subsp. <i>con-</i> <i>gesta</i>	1	2	3	3	2	2	3	4	5	5	3	3						
<i>Indigofera vicioides</i>	1	3	1	1	1	1	1	2	3	4	2	2	2					
<i>Cissus lonicerifolius</i>	1	2	2	2	1	1	1	1	3	1	2	2						
<i>Hermannia glanduligera</i>	3	2	1	3	2	1	1	1	1		2	1		3				
<i>Rhynchosia totta</i>	3	1	2		1	1	1	1	3	3	2	2	3					
<i>Phyllanthus burchellii</i>	1	5	3	1	1	3		1	3		1	2	2					
<i>Hibiscus engleri</i>	2	2	2	2	2	2	2	1		1	1	1			2			
<i>Brachiaria nigropedata</i>	2	3	1	3	1	1		1	1		2	2						
<i>Vigna unguiculata</i>	3	2	4	4	1	1	1	1			2	2						
<i>Commelina africana</i>	2		2	1	1	1	2	1			1	1						
<i>Acalypha indica</i>	1		1	2	1	1	2	1	2	2	1	1	2					
<i>Boscia albitrunca</i>	1	1	2	3	2	1	1	1	1			2						
<i>Commelina erecta</i>	2	3	1	2	2	1	2	1	1			2						
<i>Monechma monechmoides</i>	1	1	3	2	1	2	1	1	3		1	1						
<i>Enneapogon cenchroides</i>	1	1	1	3	2	1	3	4	5	2	2	2						
<i>Phyllanthus pentandrus</i>	1	1	1	1	1	1	1	2	1	4	1	3						
<i>Tephrosia polystachya</i>	1	2	5	3	1	1		1	3	3	2	3						
<i>Cassia abbreviata</i>	1	1	1		1	1			1		1	1						
<i>Schmidtia pappophoroides</i>	2	2	4	4	1						3	4						
<i>Hibiscus sidiformis</i>	1	1	1	1	1	2	1	1	2		2	2						
<i>Kyphocarpa angustifolia</i>	1	1	1	1	3			1	2	1		2						
<i>Grewia bicolor</i>	1		2	2	2	1	3	4	4	4	2	3	2					
<i>Dalbergia melanoxylon</i>	2		4	3	1		1	1	1	1	4	3	2					
<i>Pseudobrachiaria deflexa</i>		2			1	3	2	1	3		1	1						
<i>Pupalia lappacea</i>	1			2	2	3	3	1	2				2					
<i>Evolvulus alsinoides</i>	1	1	1	2	2	1		1	3	2		1						
<i>Tragus berteronianus</i>			1	1	1		3	1	1	1	1	1						
<i>Cassia mimosoides</i>	1			2		1		1			2	1						
<i>Euphorbia polycnemoides</i>	1			1	3	1		1	3	2	1	2						
<i>Crotalaria virgulata</i>		1	1	1		1		2	1									
<i>Euphorbia tetensis</i>	2		3	2				1	3	1	1	2						
<i>Maytenus heterophylla</i>			1			1	1	1	1	4	1							
<i>Cucumis anguria</i>				2		1	1	1		1	1							
<i>Corchorus asplenifolius</i>	1			3		1	1		2	2		1		3				
<i>Lantana rugosa</i>	2		1		1	1						2						
<i>Tricalysia allenii</i>	1	1		1	2				1			1						

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Ipomoea obscura</i>				1		1	2	1	1		1	1					
<i>Grewia monticola</i>			3	1	1	1		1			1	1					
<i>Mundulea sericea</i>	1		1	1	1				1		1	1					
<i>Cymbopogon excavatus</i>					1				1	1	2	1	3	2			
<i>Markhamia acuminata</i>				2	1				1		1	1					
<i>Gardenia resiniflua</i>				1	1	1	1	1	1			1					
<i>Justicia protracta</i>	1							1	1	1							
<i>Barleria affinis</i>					1				1								
<i>Stylochiton natalensis</i>	1				1	1		1									
<i>Eragrostis curvula</i>				1				1	1				1				
<i>Ipomoea pes-tigrides</i>	1	2		1				1									
<i>Zornia diphylla</i>	1	2		1	1				1			1					
<i>Clerodendron ternatum</i>	1		1	1				1	1	1	1	1					
<i>Justicia flava</i>					1			1	1			1					
<i>Manilkara mochisia</i>	1			1	1				1								
<i>Rhynchosia minima</i>	1								1		1	1					
<i>Eragrostis heteromera</i>				1				1		1							
<i>Grewia hexamita</i>		1	1	1	1	1			1		1		2				
<i>Gisekia africana</i>				1			2				1						
<i>Commiphora edulis</i>					1	1			1								
<i>Anisotes sessiliflorus</i>		1			1		1	1	1								
<i>Cardiospermum halicacabum</i>					1				1								
<i>Aspilia mossambicensis</i>	1								1			1					
<i>Dactyloctenium aegyptium</i>				1			1										
<i>Polygala wilmsii</i>	2		1		1				1		1						
<i>Calostephane divaricatum</i>				1	1				1	1							
<i>Hermibstaedia odorata</i>	1								1		1	1					
<i>Kyllinga alba</i>	1					1		1			1	1					
<i>Kohautia virgata</i>	2							1	1		1	1					
<i>Gardenia spatulifolia</i>			1	1		1											
<i>Cissus quadrangularis</i>					1	1	1	1									
<i>Stipagrostis uniplumis</i>	1			1				1	1		1						
<i>Eragrostis lehmanniana</i>				1				1	1								
<i>Leptactinia benguelensis</i>		1	1		1	1			1								
<i>Ipomoea crassipes</i>											1						
<i>Orthosiphon suffrutescens</i>								1	1								
<i>Grewia villosa</i>					1	1	1		1		1						
<i>Lippia javanica</i>								1	1		1		2				
<i>Merremia palmata</i>											1	1					
<i>Endostemon tenuiflorus</i>									1	1							
R <i>Setaria holstii</i>													4	3	2		
<i>Piliostigma thonningii</i>													3				
<i>Hyparrhenia rufa</i>													3				
<i>Helichrysum miconiifolium</i>													3				

PLANT SPECIES	COMMUNITIES																
	SANDVELD					COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1		2.2	3	4	1.1	1.2	1.3
<i>Ipomoea papilio</i>						1							3				
<i>Acacia gerrardii</i>											1		2				
S <i>Acacia borleae</i>														5			
<i>Tetrapogon mossambicensis</i> ..								1						5			
<i>Cephalocroton mollis</i>										1				5			
<i>Ruellia patula</i>				1			1	1	1		1	1		5			
<i>Brachiaria erucaeformis</i>														3			
T <i>Sesbania sesban</i>															4		
<i>Fuirena pubescens</i>															3		
U <i>Acacia albida</i>																	5
<i>Ficus sycomorus</i>																	4
<i>Acacia robusta</i>																	4
<i>Trichilia emetica</i>																	4
<i>Diospyros mespiliformis</i>																	4
<i>Hypoestes verticillaris</i>																	3
<i>Abutilon angulatum</i>																	3
<i>Tabernaemontana elegans</i>	1				1												3
V <i>Setaria sphacelata</i>									1			1	2	3	3		3
<i>Ischaemum afrum</i>														5	4		2
<i>Ischaemum brachyatherum</i> ...														3	2		1
<i>Panicum meyerianum</i>															4	3	4
<i>Echinochloa pyramidalis</i>															3		2
<i>Acacia xanthophloea</i>																3	1
<i>Sporobolus consimilis</i>																2	2
<i>Xanthocercis zambeziaca</i>																3	1
<i>Kigelia africana</i>																2	1
<i>Cyperus fenzelianus</i>																	2
<i>Croton megalobotrys</i>																	1
<i>Chloris gayana</i>	1																1
W <i>Panicum maximum</i>	4	5	5	5	4	3	5	4	4	1	3	4	2		4	5	3
<i>Digitaria eriantha</i>	5	4	5	5	5	2	1	3	4	4	5	5	2	3	3	4	
<i>Hibiscus micranthus</i>	1	1	2	2	3	3	3	4	5	3	1	4			2		
<i>Lonchocarpus capassa</i>	1	1	3	1	1	1	1	1			2		3		4	4	2
<i>Spirostachys africana</i>	1	3	1	1	1		1	2							4		1
<i>Combretum imberbe</i>				1			1	1	1	1	3	1	2		3	3	2
<i>Solanum panduraeforme</i>	2			2	2	2	1	2	2	1	2	3			2		1
<i>Dichrostachys cinerea</i>	2	3	1	3	2	1	1	1	2	2	2	3	4		2		1
<i>Combretum mossambicensis</i> ..	1	2	2	3	1	1	1	1	2	1		2	2				1
<i>Acacia nigrescens</i>	1			2	2		2	3	3	4	2	4	3		4		
<i>Securinega virosa</i>		2	1	1	1		1	1	1		1	1		5			1

PLANT SPECIES	COMMUNITIES																	
	SANDVELD						COLOPHOSPER- MUM MOPANE						DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4	
<i>Vernonia fastigiata</i>	4			1	2	2	1	1	2	1	3	1		5				
<i>Cenchrus ciliaris</i>			1					1	2		2	1					1	
<i>Achyranthes aspera</i>	1			1	1	3	1	1	1							5	1	
<i>Indigofera rhytidocarpa</i>	1	1		2			3	1	1	2	1	1						
<i>Lannea stuhlmannii</i>		2	1	1			1	1	1		1	1			2			
<i>Leucas glabrata</i>	1		1	2	1	1	1	1	2								1	
<i>Melhania forbesii</i>	1	1	3	2	1			2	1	1	1	2					1	
<i>Monechma divaricatum</i>			1	2			1	1										
<i>Sclerocarya caffra</i>	1	1	2	1	1				1		1	1			2			
<i>Rhynchelytrum villosum</i>			1	2	1	2		1	2	3	1	1	2					
<i>Commiphora mollis</i>				2				1	2	2		1						
<i>Becium obovatum</i>				1		1	1	1	3			1						
<i>Asparagus setaceus</i>	1			1	1	2		2	1	1		1		3				
<i>Corchorus kirkii</i>		2	2	1	1			1	1		1	1			3		1	
<i>Tragia rupestris</i>	1		1	1	1			1	1		1	2			2		1	
<i>Grewia flavescens</i>		2		1	1	1		1								2		
<i>Maytenus senegalensis</i>				1									2				1	
<i>Leonotis nepetifolia</i>	2			1	1	1							2				1	
<i>Pterocarpus rotundifolius</i>											1		2					
<i>Ceratotheca triloba</i>				1			1		1		1				2			
<i>Barleria transvaalensis</i>							1	1	1									
<i>Peltophorum africanum</i>	2				1			1					2					
<i>Hemizygia bracteosa</i>	1	1	2	1	1					1		1			2			
<i>Albizia harveyi</i>									1		1	1			2			
<i>Abutilon guineense</i>				1	1		1	1	1								1	
<i>Ziziphus mucronata</i>				1			1	1		1		1					1	
<i>Melhania rehmannii</i>				1	1			1			1						1	
<i>Cyperus</i> sp.					1		1	1		1					2			
<i>Ormocarpum trichocarpum</i>								1			1		2		2			
<i>Abutilon ramosum</i>							1				1		2				1	
<i>Indigofera schimperii</i>	1				1						1	1		3	2			
<i>Cassia petersiana</i>	1	1	1	1							1		2					

Quaternary period (Van Rooyen, 1978). These communities are jointly characterised by species group H (Table 1) and can be subdivided as follows:

1. The *Terminalia sericea*—*Pteleopsis myrtifolia* tree savanna
 - 1.1 The *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna
 - 1.2 The *Baphia massaiensis*—*Guibourtia conjugata* thicket
 - 1.3 The *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna
 - 1.4 The *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna

2. The *Croton gratissimus*—*Phyllanthus reticulatus* tree savanna
 - 2.1 The *Kirkia acuminata*—*Azelia quanzensis*—*Combretum apiculatum* tree savanna
 - 2.2 The *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest
3. The Rocky Outcrop community
4. The Diabase community

The Rocky Outcrop (3) and Diabase community (4) were only described physiognomically. The four communities of the first group (paragraphs 1.1, 1.2, 1.3, 1.4) are found mainly on the plains with deep sandy soils which are characterised by the following factors: low pH, leached deep sandy soil, high electrical resistance and a low percentage of stone covering. The altitude is normally higher than that of the surrounding *Colophospermum mopane* communities. The two communities of the second group (2.1, 2.2) are characterised by the following habitat factors: shallow, rocky, sandy soil and moderate to steep slopes. The pH and electrical resistance of the soil varies greatly.

The Rocky Outcrop community (3) is characterised by hills and inselbergs built up of Cave Sandstone while the Diabase community (4) is found on diabasic sills characterised by a dark red-brown clay soil.

1. The *Terminalia sericea*—*Pteleopsis myrtifolia* tree savanna. The four communities (paragraphs 1.1, 1.2, 1.3 and 1.4) within this savanna are characterised by species groups A, B, C and D respectively (Table 1). These communities are related to each other by the mutual presence of species group D. Community 1.4 is distinguished from communities 1.1, 1.2 and 1.3 by the absence or poor representation of species groups A, B and C (Table 1).

The habitat of the following four communities are characterised in general by the following factors:

- Community 1.1: Red-brown fine textured sandy soil on the plains and on rocky north-facing slopes.
- Community 1.2: Deep red coarse textured sandy soil, strongly leached, with a very low pH, and stones absent on the soil surface.
- Community 1.3: } The habitat of these two communities are very similar. Fine to
 1.4: } medium textured brown sandy soil with a low pH and with
 } stones normally absent on the soil surface.

A prominent feature within community 1.3 is the large number of pans such as Shirombe, Magwitsi, Wambiyane, Matlakuza and Klawer pan that occur in the western part (Van Rooyen *et al.*, (1981a).

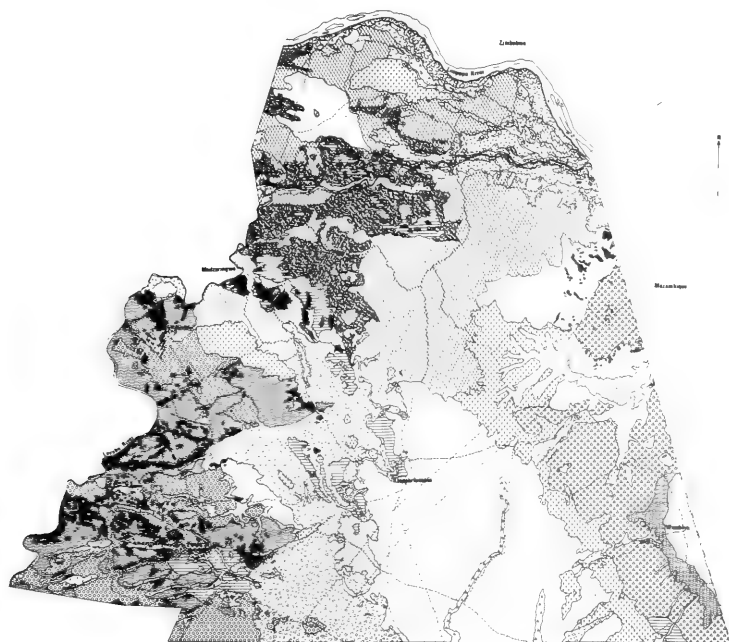


FIG. 1.

Vegetation map of the Punda Milia—Pafuri—Wambya area in the Kruger National Park.

1.1 The *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna

This community occurs mainly on Waterberg Sandstone at 400 to 555 m above sea level on plains and on slopes with a gradient up to 10° and covers the broken country around Punda Milia, from the Levubu River in the west to Xantangelane in the east. This community usually occurs on the plains and on the north-facing slopes which are warmer and drier than the south facing slopes (Figs 1 & 2).

The Waterberg Sandstone weathers to a red brown to a dark red-brown fine textured sand or loamy sand. The soil layer varies from 30 mm to more than 1 m deep. Up to 60 % of the soil surface is covered by stones and the topsoil is apedal with a loose consistency. The pH of the strongly leached to normal soil ranges from 5.2 to 6.2. Carbonates are usually absent.



BURKEA AFRICANA-PSEUDOLACHNOSTYLIS MAPROUNEIFOLIA TREE SAVANNA

BAPHIA MASSAIENSIS-GUIBOURTIA CONJUGATA THICKET



BAPHIA MASSAIENSIS-GUIBOURTIA CONJUGATA THICKET



BAPHIA MASSAIENSIS-XYLIA TORREANA TREE SAVANNA



XERODERRIS STUHLMANNII-COMBRETUM APICULATUM TREE SAVANNA



TERMINALIA SERICEA-POGONARTHRIA SQUARROSA TREE SAVANNA

KIRKIA ACUMINATA-AFZELIA QUANZENSIS-COMBRETUM APICULATUM TREE SAVANNA



KIRKIA ACUMINATA-AFZELIA QUANZENSIS TREE SAVANNA



COMBRETUM APICULATUM-KIRKIA ACUMINATA TREE SAVANNA



ANDROSTACHYS JOHNSONII-CROTON PSEUDOPULCHELLUS DRY FOREST



ROCKY OUTCROP COMMUNITY



MIXED ROCKY OUTCROP COMMUNITY AND ANDROSTACHYS JOHNSONII-CROTON PSEUDOPULCHELLUS DRY FOREST

COLOPHOSPERMUM MOPANE-ACACIA TORTILIS-UROCHLOA MOSAM-BICENSIS TREE SAVANNA



ACACIA TORTILIS TREE SAVANNA



ACACIA SENEGAL SHRUB SAVANNA



SALVADORA ANGUSTIFOLIA SHRUB SAVANNA



COLOPHOSPERMUM MOPANE-EUCLEA DIVINORUM-ENTEROPOGON
MACROSTACHYUS TALL TREE SAVANNA



COLOPHOSPERMUM MOPANE-COMMIPHORA GLANDULOSA-SEDDERA
CAPENSIS OPEN TREE SAVANNA



COLOPHOSPERMUM MOPANE-ENNEAPOGON SCOPARIUS SHRUB SAVANNA



COLOPHOSPERMUM MOPANE-THEMEDA TRIANDRA SHRUB SAVANNA



COLOPHOSPERMUM MOPANE-COMBRETUM APICULATUM-DIGITARIA
ERIANTHA OPEN TREE SAVANNA



DIABASE COMMUNITY



ACACIA BORLEAE-ISCHAEMUM AFRUM SHRUB THICKET



COMBRETUM IMBERBE-FUIRENA PUBESCENS OPEN TREE SAVANNA



ACACIA ALBIDA-FICUS SYCOMORUS RIVERINE FOREST

ACACIA XANTHOPHLOEA-PANICUM MEYERIANUM OPEN TREE SAVANNA



ACACIA XANTHOPHLOEA OPEN TREE SAVANNA



SPOROBOLUS CONSIMILIS GRASSLAND



PAN COMMUNITIES



INTERNATIONAL BORDERS



ROADS



RIVERS



FIG. 2.

The *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna on Waterberg Sandstone.

Floristic composition

Trees, among which *Burkea africana*, *Pteleopsis myrtifolia* and *Pseudolachnostylis maprouneifolia* are the most striking, grow up to 10 m high. Shrubs and sparse shrubs reach up to 3 m and include species such as *Hymenocardia ulmoides*, *Xylopia odoratissima*, *Bauhinia galpinii*, *Diplorhynchus condylocarpon* and *Pteleopsis myrtifolia*. Two species, namely *Ochna pulchra* and *Holarhena pubescens* are characteristic for this community only. In the study area the latter species together with *Burkea africana* are restricted to this community. Other conspicuous woody species are *Combretum collinum*, *C. zeyheri*, *Hexalobus monopetalus*, *Peltophorum africanum*, *Monodora junodii* and *Dalbergia melanoxylon*. A few species with a tropical distribution such as *Acacia polyacantha* subsp. *campylacantha*, *Xylopia odoratissima*, *Crossopteryx febrifuga* and *Drypetes gerrardii* (Van Wyk, 1972, 1974) are found in this community. *Pterocarpus angolensis*, *Heteropyxis natalensis*, *Turraea nilotica*, *Peltophorum africanum*, *Manilkara mochisia*, *Combretum molle* and *Cryptolepis oblongifolia* are less conspicuous, yet occur scattered throughout this community.

The herbaceous component is dominated by *Andropogon gayanus* and *Fimbristylis hispidula*, while *Digitaria eriantha* and *Panicum maximum* often grow in association with them. Other widespread herbaceous species in this community are *Pogonarthria squarrosa*, *Tricholaena monachne*, *Eragrostis pallens*, *Aristida argentea*, *Hermannia glanduligera*, *Brachiaria nigropedata* and *Vigna unguiculata*.

Structure

The structural analysis of the woody component of the community is given in Tables 2 and 3 as well as in Figures 9 and 10.

The highest total percentage canopy spread is found in the 2 m stratum, while the values for the 1 m and 3 m strata are also relatively high (Table 2). In the strata above 3 m the canopy spread is relatively low. The total percentage canopy spread in the 2 m stratum (13.83 %) can mainly be attributed to species of the 3 m height class (6.22 %). Up to the 3 m stratum, shrubs have the highest total percentage canopy spread. In the 2 m stratum *Hymenocardia ulmoides*, *Bauhinia galpinii*, *Diplorhynchus condylocarpon* and *Pteleopsis myrtifolia* have high percentage canopy spread values, while in the >6 m stratum *Pseudolachnostylis maprouneifolia*, *Burkea africana* and *Pteleopsis myrtifolia* have a relatively high percentage canopy spread (Table 3).

Most of the individuals up to 3 m are shrubs or sparse shrubs whereas the higher height classes are dominated by trees (Table 2). *Pseudolachnostylis maprouneifolia* (2.46 %) and *Bauhinia galpinii* (2.32 %) have the highest percentage apparent canopy cover while *Holarrhena pubescens* (273 indiv/ha) and *Diplorhynchus condylocarpon* (110 indiv/ha) have the highest densities (Table 3).

1.2 The *Baphia massaiensis*—*Guibourtia conjugata* thicket

This thicket is situated on the eastern border of the Kruger National Park, from south of Shirombe to just south of Matlakuze Pan and stretches westwards more or less to Wambiya Pan (Figs 1 & 3). This community lies on a sandy plateau between 475 and 532 m above sea level. The medium to coarse-textured sandy soil is brown, dull brown to dark red-brown in colour and deeper than 1 m. Stones seldom appear on the soil surface. The strongly leached topsoil is apedal with a loose consistency and has a pH ranging from 4.3 to 5.5. Carbonates are absent in the topsoil.

Floristic composition

In those parts where *Baphia massaiensis* and *Guibourtia conjugata* are the most abundant species a dense thicket 3 to 4 m high is formed. The western parts of the community is a tree savanna with species such as *Azelia quanzensis* becoming up to 10 m high. Other widespread species are *Xylia torreana*, *Combretum celastroides*, *Hugonia orientalis*, *Pteleopsis myrtifolia*, *Vitex amboniensis*,

TABLE 2.
Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv/ha) in different height classes of woody plant species in the *Burkea africana*—*Pseudolachnostylis maprounifolia* tree savanna.

Stratum (m)	Percentage canopy spread										Mean number of indiv/ha			
	Total*	Growth form			Height class					Height class (m)	Total	Growth form		
		Tree	Sparse shrub	Shrub	>6	4-5 m	3 m	2 m	1 m			Tree	Sparse shrub	Shrub
>6	2.38	2.08	0.25	0.05	2.38					>6	19	15	4	
4-5	4.90	2.78	1.57	0.55	2.16					4-5	72	33	27	12
3	10.20	2.90	3.54	3.76	1.10					3	214	49	93	72
2	13.83	2.30	4.72	6.81	0.27		5.24			2	480	146	189	145
1	12.92	1.89	3.75	7.28	0.08		3.71	5.29	3.13	1	542	171	219	152
0.5	9.05	0.96	2.39	5.70	0.03		1.72	3.15	2.37	0.5	825	233	387	205
										Total	2 152	647	919	586

*Figures in this column are referred to in the text as "Total percentage canopy spread" values.

TABLE 3.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna.

Plant species*	p.a.c.	indiv/ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
<i>Pseudolachnostylis maprouneifolia</i>	2,46	69	0,73	1,42	1,48	0,88	0,60	0,44
<i>Bauhinia galpinii</i>	2,32	81			0,60	1,40	1,60	1,40
<i>Hymenocardia ulmoides</i>	2,21	101		0,13	1,35	2,06	1,48	0,75
<i>Prelopsis myrsifolia</i>	2,16	76	0,37	0,51	0,97	1,05	0,84	0,38
<i>Diplorhynchus condylocarpon</i>	2,08	110	0,06	0,17	0,63	1,36	1,37	1,08
<i>Holarrhena pubescens</i>	1,84	273		0,32	0,40	0,51	0,81	0,66
<i>Burkea africana</i>	1,39	94	0,51	0,39	0,37	0,32	0,27	0,18
<i>Heteropogon natalensis</i>	1,05	25			0,95	0,75	0,53	0,13
<i>Terminalia sericea</i>	0,79	28	0,17	0,32	0,22	0,33	0,22	0,04
<i>Combretum collinum</i>	0,79	51	0,04	0,23	0,24	0,50	0,38	0,16

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.).



FIG. 3.

The *Baphia massaiensis*—*Guibourtia conjugata* thicket in the Wambya area.

Alchornea laxiflora, *Grewia microthyrsa*, *Ptaeroxylon obliquum*, *Heinsia crinita*, *Zygoon graveolens* and *Strychnos madagascariensis*.

The *Baphia massaiensis*—*Guibourtia conjugata* thicket is an unique vegetation type. Tropical species such as *Baphia massaiensis*, *Drypetes mossambicensis*, *Pterocarpus lucens* subsp. *antunesii* and *Paropsia braunii* are found nowhere else within the Republic of South Africa. Other species with tropical affinities (Van Wyk, 1972) are: *Guibourtia conjugata*, *Hugonia orientalis*, *Pteleopsis myrtifolia*, *Xylia torreana* and *Cleistanthus schlechteri*. Some of the more widespread species are *Zanthoxylum davyi*, *Ochna* spp., *Ehretia amoena*, *Anisotes sessiliflorus*, *Boscia foetida* subsp. *rehmanniana* and *Conostomium zoutpansbergensis*.

In Figure 1 the community is subdivided into the *Baphia massaiensis*—*Guibourtia conjugata* thicket and the *Baphia massaiensis*—*Xylia torreana* tree savanna. Within the latter community *Balanites maughamii*, *Xylia torreana*, *Guibourtia conjugata*, *Spirostachys africana* and *Drypetes mossambicensis* are the most striking trees. Farrell (1968) described a related community in the vicinity of Malvernia in southeastern Zimbabwe with conspicuous species such as *Baphia massaiensis*, *Guibourtia conjugata*, *Pterocarpus lucens* subsp. *antunesii*, *Strychnos madagascariensis* and *Pteleopsis myrtifolia*.

The herbaceous component is poorly developed and herbs are often completely absent underneath the dense shrubs. *Eragrostis pallens*, *Digitaria eriantha* and *Panicum maximum* are the most important herbaceous species while *Phyllanthus burchellii*, *Merremia tridentata*, *Perotis patens*, *Commelina erecta*, *Borreria scabra* and *Tricholaena monachne* are frequently found.

Structure

The structural analysis of this community is given in Tables 4 and 5 as well as in Figures 9 and 10. The highest total percentage canopy spread is found in the 2 m stratum (26,32 %) while those of the 3 m stratum (19,78 %) and the 1 m stratum (19,18 %) are also relatively high (Table 4). The total percentage canopy spread of the remaining strata are relatively low. The high value for the 2 m stratum can be attributed mainly to species of the 3 m height class. The species contributing significantly to the canopy spread in the 2 m stratum are *Baphia massaiensis*, *Guibourtia conjugata* and *Combretum celastroides* (Table 5). Species of the >6 m height class do not contribute much to the canopy spread in the 0,5 and 1 m strata (Table 4).

Density remains more or less constant from the 0,5 m up to the 3 m height class, with a sharp decrease in the taller height classes. In spite of the large number of individuals in the 0,5 stratum, the total percentage canopy spread is



FIG. 4

The *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna in the Wambiya area

TABLE 5.
Percentage canopy spread in different strata; mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy (p.a.c.) of a few species* in the *Baphia massaiensis*—*Guibourtia conjugata* thicket.

Plant species*	p.a.c.	indiv/ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
<i>Baphia massaiensis</i>	9,47	326		0,33	5,04	8,02	6,09	2,48
<i>Guibourtia conjugata</i>	8,85	345	0,50	0,99	6,17	6,70	3,80	1,13
<i>Combretum apiculatum</i>	2,62	123	0,68	1,99	1,89	0,98	0,28	0,12
<i>Ptaeroxylon obliquum</i>	1,97	63			0,87	0,92	0,46	0,03
<i>Combretum celastroides</i>	1,95	88			0,39	1,53	0,98	0,31
<i>Cleistanthus schlechteri</i>	1,35	81				0,87	0,96	0,51
<i>Combretum collinum</i>	1,24	42			0,71	0,82	0,50	0,24
<i>Spirostachys africana</i>	1,15	8			0,27	0,11	0,01	
<i>Dichrostachys cinerea</i>	1,08	122	1,03	1,04	0,67	0,42	0,49	0,27
<i>Hexalobus monopetalus</i>	1,07	253				0,67	0,72	0,59

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.).

low. Sparse shrubs are numerous in the 0,5 m and 1 m height classes, whereas the 2 m, 3 m and 4–5 m height classes are characterised mainly by shrubs (Table 4.)

Baphia massaiensis (9,47 % and 326 indiv/ha) and *Guibourtia conjugata* (8,85 % and 345 indiv/ha) have the highest percentage apparent canopy cover and density, while *Hexalobus monopetalus* (253 indiv/ha) is also present in large numbers (Table 5).

1.3 The *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna

This tree savanna borders on the *Baphia massaiensis*–*Guibourtia conjugata* thicket to the east, the *Colophospermum mopane*–*Combretum apiculatum*–*Digitaria eriantha* open tree savanna to the west and the *Colophospermum mopane*–*Enneapogon scoparius* shrub savanna to the north. It occurs on a sandy plateau between 400 and 475 m above sea level (Figs 1 & 4).

The fine to medium textured sand to sandy loam soil is dark red-brown to dull brown and is more than 1 m deep. No stones are found on the surface and the strongly leached topsoil is apedal with a loose consistency. The pH ranges from 5,0 to 6,4 and carbonates are absent.

Floristic composition

Trees become up to 10 m high and the most abundant species are *Sclerocarya caffra*, *Xeroderris stuhlmannii* and *Combretum apiculatum*, while *Adansonia digitata* and *Azelia quanzenensis* are very conspicuous but occur more scattered. Shrubs and sparse shrubs, e.g. *Terminalia sericea*, *Combretum apiculatum* and *C. collinum* are 2 to 3 m high. Other associated woody species include *Dalbergia melanoxylon*, *Strychnos madagascariensis*, *Balanites maughamii*, *Guibourtia conjugata*, *Vangueria infausta*, *Grewia monticola* and *Boscia albitrunca*. Characteristic species in the herbaceous stratum are *Aristida stipitata*, *A. junciformis*, *Indigofera inhambanensis*, *Limeum dinteri*, *Macrotyloma axillare* and *Pavonia burchellii*. Associated species are *Digitaria eriantha*, *Tephrosia polystachya*, *Schmidtia pappophoroides*, *Vigna unguiculata* and *Tricholaena monachne*.

The community covers the biggest part of the Wambiya area and a characteristic feature is the large number of termitaria occurring locally. Species such as *Spirostachys africana*, *Diospyros mespiliformis*, *Euclea divinorum*, *Capparis tomentosa*, *Panicum maximum*, *Chloris roxburghiana* and *Cenchrus ciliaris* thrive on these termitaria. Farrell (1968) described a related community in southeastern Zimbabwe which is characterised by *Combretum apiculatum* and the associated species are *Pteleopsis myrtilifolia*, *Strychnos madagascariensis*, *Azelia quanzenensis*, *Xeroderris stuhlmannii*, *Sclerocarya caffra* and *Pseudolachnostylis maprouneifolia*.

TABLE 6.
Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv/ha) in different height classes of woody plant species in the *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna

Stratum (m)	Percentage canopy spread							Mean number of indiv/ha			
	Total*	Growth form			Height class				Total	Growth form	
		Tree	Sparse shrub	Shrub	>6 m	4-5 m	3 m	2 m	1 m	0,5 m	Height class (m)
>6	0,59	0,40	0,13	0,06	0,59						>6
4-5	3,59	1,15	1,62	0,82	0,78	2,81					4-5
3	8,45	2,37	3,94	2,14	0,56	3,11	4,78				3
2	9,71	1,69	4,41	3,61	0,14	1,81	4,54	3,22			2
1	7,02	0,80	2,71	3,51	0,01	0,51	2,35	2,87	1,28		1
0,5	4,20	0,22	1,22	2,76		0,21	0,81	1,42	1,09	0,67	0,5
											Total
											1 337
											254
											6,35
											448

*figures in this column are referred to in the text as "Total percentage canopy spread" values.

TABLE 7.
Percentage canopy spread in different strata: mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Xerodermis stuhlmannii*—*Combretum apiculatum* tree savanna.

Plant species*	p.a.c.	indiv/ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0.5
<i>Combretum apiculatum</i>	4.68	231	0.15	1.85	3.34	2.96	1.34	0.36
<i>Terminalia sericea</i>	2.40	114	0.07	0.68	2.13	1.93	1.01	0.36
<i>Combretum collinum</i>	1.25	58		0.01	0.54	0.85	0.76	0.50
<i>Pteleopsis myrtifolia</i>	0.90	122		0.11	0.19	0.41	0.40	0.47
<i>Strychnos madagascariensis</i>	0.81	169	0.03	0.06	0.41	0.57	0.44	0.22
<i>Dalbergia melanoxylon</i>	0.68	122		0.01	0.14	0.58	0.47	0.25
<i>Guibourtia conjugata</i>	0.55	20	0.06	0.09	0.17	0.33	0.40	0.21
<i>Pseudolachnostylis maprouneifolia</i>	0.45	18	0.04	0.24	0.34	0.29	0.20	0.08
<i>Dalbergia nitida</i>	0.29	6			0.17	0.29	0.18	0.11
<i>Sclerocarya caffra</i>	0.29	14	0.11	0.26	0.17	0.01	0.01	0.02

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.).



FIG. 5.

The *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna on deep sandy soils.

Structure

The structural analysis of this community is given in Tables 6 and 7 as well as in Figures 9 and 10. The 2 m and 3 m strata have the highest total percentage canopy spread (Table 6). Species such as *Combretum apiculatum*, *Terminalia sericea* and *Combretum collinum*, contribute considerably to these values (Table 7). In the 0,5 m and 1 m strata shrubs have the highest total percentage canopy, whereas sparse shrubs have the highest values in the 2 m and 4–5 m strata (Table 6).

The highest density is found in the 0,5 m, 1 m and 2 m height classes. Sparse shrubs are most numerous in the 0,5 m and 2 m height classes, whereas shrubs are most numerous in the 1 m height class.

Only a few trees and sparse shrubs occur in the >6 m height class (Table 6).

Species with high percentage apparent canopy cover values are *Combretum apiculatum* (4,68%) *Terminalia sericea* (2,40%) and *Combretum collinum* (1,25%) while high densities were calculated for *Combretum apiculatum* (231 indiv/ha). *Strychnos madagascariensis* (169 indiv/ha), *Pteleopsis myrtifolia* (122 indiv/ha) and *Dalbergia melanoxylon* (122 indiv/ha) (Table 7).

1.4 The *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna

This savanna lies at 305 to 475 m above sea level in the Punda Milia area, the northwestern Cave Sandstone area and in parts of the Wambya Sandveld. It is found on plains, plateaus and on moderate western, southern and northeastern slopes with a gradient up to 6° (Figs 1 & 5).

The community occurs on Waterberg Sandstone, Cave Sandstone, shale and aeolian sand. The fine to medium-textured brown to dark brown sand, to sandy loam soil varies from 120 mm to more than 1 m deep. Up to 20% of the soil surface may be covered with stones. The topsoil is apedal, has a loose consistency, is strongly leached and has a pH between 5.4 and 6.3. Carbonates are locally present in low concentrations.

Floristic composition

Most of the trees are 4 to 7 m high with a few reaching up to 12 m. Conspicuous tree species are *Terminalia sericea*, *Lannea stuhlmannii*, *Kirkia acuminata* and *Sclerocarya caffra*. In the 2 m and 3 m strata the most important shrubs and sparse shrubs are *Combretum collinum*, *Xeromphis obovata*, *Combretum zeyheri* and *Strychnos madagascariensis*. Associated species include *Combretum apiculatum*, *Hippocratea crenata*, *Dalbergia melanoxylon*, *Boscia albitrunca*, *Lonchocarpus capassa*, *Dichrostachys cinerea* and *Combretum mossambicensis*.

The presence of species such as *Terminalia sericea*, *Combretum collinum*, *Strychnos madagascariensis* and *Xeroderris stuhlmannii* in the Pafuri area indicate the affinities between this community and the *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna. Physiognomically and structurally these two communities are very similar.

The herbaceous component is characterised by *Panicum maximum* and *Digitaria eriantha* with high canopy cover values, as well as by *Schmidtia pappophoroides*, *Crotalaria sphaerocarpa* and *Pogonarthria squarrosa*. A few species such as *Vigna unguiculata*, *Brachiaria nigropedata*, *Merremia tridentata*, *Tephrosia polystachya*, *Hermannia glanduligera* and *Perotis patens* are found scattered throughout the community.

Structure

The structural analysis of the woody component of the community is given in Tables 8 and 9 as well as in Figures 9 and 10.

The highest total percentage canopy spread is found in the 2 m stratum (11.39%). Species of the 3 m height class contribute the most to this value. The highest total percentage canopy spread in the strata up to 2 m is due to shrubs, in the 3 m stratum it is sparse shrubs and in the 4–5 m and >6 m strata it is trees, that contribute most to the total percentage canopy spread. Species of the >6 m stratum contribute little to the 0.5 m, 1 m and 2 m strata (Table 8). In the 2 m and 3 m strata *Combretum apiculatum*, *C. collinum* and *Terminalia sericea*

TABLE 2.

Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv./ha) in different height classes of woody plant species in the *Terminalia sericea*—*Pogonanthia squarrosa* tree savanna.

[illegible]

*Figures in this column are referred to in the text as "Total percentage canopy spread" values.

TABLE 9.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna.

Plant species*	p. a. c.	indiv/ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
Combretum apiculatum	3,43	155	0,10	1,14	2,30	2,16	1,03	0,37
Combretum collinum	2,75	62	0,04	0,40	1,54	2,09	1,63	1,06
Terminalia sericea	2,23	57	0,32	0,91	1,09	1,01	0,71	0,30
Hippocratea crenata	1,64	100				0,12	0,16	1,58
Pteleopsis myrtilifolia	1,24	48		0,22	0,72	0,98	0,53	0,22
Combretum zeyheri	1,21	67		0,11	0,67	0,92	0,67	0,41
Strychnos madagascariensis	0,70	112			0,13	0,49	0,57	0,39
Grewia bicolor	0,57	31			0,05	0,41	0,53	0,29
Dalbergia melanoxylon	0,43	86			0,01	0,16	0,26	0,26
Boscia albitrunca	0,37	21	0,04	0,11	0,23	0,08	0,07	0,08

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.).

have high total percentage canopy spread values, while *Terminalia sericea* has the highest value in the >6 m stratum (Table 9).

Plants of the 0,5 m height class have the highest density and the density decreases progressively up to the >6 m height class (Table 8). *Combretum apiculatum* (155 indiv/ha) and *Strychnos madagascariensis* (112 indiv/ha) attain high densities in the community (Table 9) whereas *Combretum apiculatum* (3,43 %), *C. collinum* (2,75 %) and *Terminalia sericea* (2,23 %) have high percentage apparent canopy cover values.

2. The *Croton gratissimus*—*Phyllanthus reticulatus* tree savanna

This tree savanna is characterised by species groups E, F & G. It occurs on steep rocky slopes and in "kloofs" in the sandstone areas of the Waterberg and Karoo Systems, as well as on the Malvernia Formation south of Pafuri.

Two communities (2.1, 2.2) can be distinguished and are characterised by species group E and F respectively. The presence of species group G (Table 1) indicates affinities between the *Kirkia acuminata*—*Azelia quanzensis*—*Combretum apiculatum* tree savanna (2.1) and the *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest (2.2). The two communities often appear in association with each other on the same slope. The affinities of community 2.1 to the other Sandveld communities are shown by species groups G and H and the absence of species such as *Pseudolachnostylis maprouneifolia*, *Hexalobus monopetalus*, *Strychnos madagascariensis* and *Guibourtia conjugata* is noteworthy. Species group H also reveals the relationship between the *Croton gratissimus*—*Phyllanthus reticulatus* tree savanna (2) and the *Terminalia sericea*—*Pteleopsis myrtifolia* tree savanna (1).

The habitats of both these communities are very similar except that community 2.1 is mainly found on steep south-facing slopes whereas community 2.2 is not influenced by aspect. Both communities are characterised by a shallow, stony, dark red-brown fine-textured soil.

2.1 The *Kirkia acuminata*—*Azelia quanzensis*—*Combretum apiculatum* tree savanna

This community is found in the Punda Milia area between 305 and 555 m above sea level, mainly on steep south-facing slopes with a gradient up to 31° (Figs 1 & 6). The southern slopes are more cooler and moist than the northern slopes as a result of the moist south-eastern winds from the Indian ocean.

Weathering of the Waterberg and Cave Sandstone in this area results in a dark red-brown fine-textured loamy sand to sandy clay loam soil. In general the soil is shallow (100–300 mm deep) and 8 to 40 % of the soil surface is covered with stones. The soil is apedal with a loose consistency and has a pH of 4.8 to 7.2. In some places the soil is strongly leached and carbonates are locally present in a low concentration.

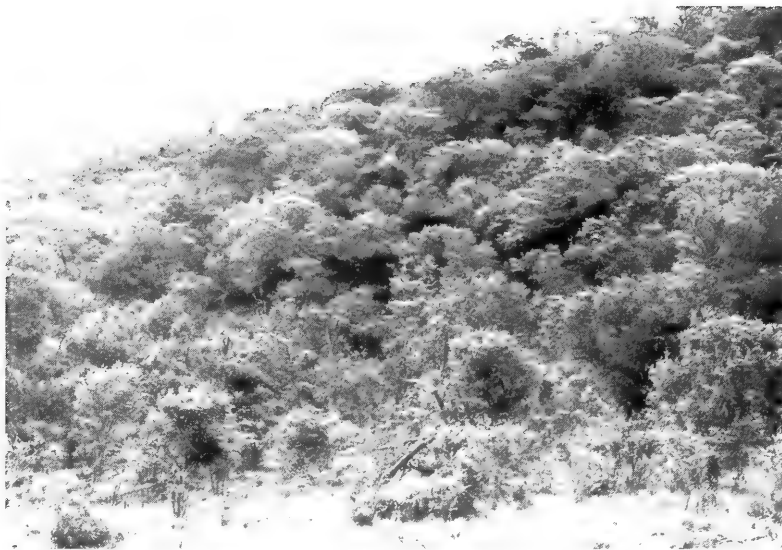


FIG. 6.

The *Kirkia acuminata*—*Afzelia quanzensis*—*Combretum apiculatum* tree savanna against a south-facing slope near Punda Milia.

Floristic composition

The trees become up to 12 m high and the conspicuous species are *Afzelia quanzensis*, *Kirkia acuminata*, *Croton gratissimus*, *Guibourtia conjugata* and *Combretum apiculatum*. Shrubs and sparse shrubs grow up to 3 m high and include species such as *Combretum apiculatum*, *Hymenocardia ulmoides*, *Diplorhynchus condylocarpon*, *Monodora junodii* and *Hexalobus monopetalus*. Species such as *Combretum zeyheri*, *Strychnos madagascariensis*, *Rhoicissus revoilii*, *Bridelia mollis*, *Phyllanthus reticulatus*, *Alchornea laxiflora*, *Maytenus mossambicensis* and *Artabotrys brachypetalus* occur widespread throughout the community.

Under the trees the herbaceous species have a low canopy cover but they are more dense in the open patches. Characteristic species are *Pellaea viridis*, *P. calomelanos*, *Euphorbia polycnemoides*, *Kyphocarpa angustifolia*, *Panicum maximum* and *Digitaria eriantha*. Other less common species are *Asparagus falcatus*, *Indigofera lupatana*, *Panicum deustum*, *Achyranthes sricula*, *Triumfetta pentandra* and *Crabbea velutina*.

A number of species showing tropical affinities occur in this community. These species, such as *Warburgia salutaris*, *Wrightia natalensis*, *Entandrophragma caudatum*, *Gyrocarpus americanus*, *Albizia tanganyicensis*, *Schrebera argyrotricha* and *Steganothaenia araliacea* are relatively scarce or absent in other parts of the Kruger National Park.

A number of species such as *Brachylaena huillensis*, *Elephantorrhiza burkei*, *Rhus leptodictya*, *Acacia erubescens*, *Landolphia kirkii* and *Canthium huillense* are not common, yet are often locally conspicuous. On the densely vegetated slopes and in the "kloofs" the following species are common:

<i>Cussonia spicata</i>	<i>Strychnos usambarensis</i>
<i>Ficus sansebarica</i>	<i>Acacia ataxacantha</i>
<i>Urera tenax</i>	<i>Vepris reflexa</i>
<i>Erythrina lysistemon</i>	<i>Brachylaena huillensis</i>
<i>Pouzolzia hypoleuca</i>	<i>Heteropyxis natalensis</i>

On the drier north-facing slopes this community differs from the savanna on the south-facing slopes. *Combretum apiculatum* is more striking on the north-facing slopes and as can be seen in Figure 1, the community can be subdivided into the *Kirkia acuminata*—*Afzelia quanzensis* tree savanna and the *Combretum apiculatum*—*Kirkia acuminata* tree savanna.

Structure

The structural analysis of this community is given in Tables 10 and 11 as well as in Figures 9 and 10. The vegetation up to a height of 3 m is dense (Table 10) and yields high total percentage canopy spread values for these strata: 14,85 % for the 3 m stratum, 14,50 % for the 2 m stratum and 11,20 % for the 1 m stratum. In the >6 m stratum the total percentage canopy spread is 4,25 % and it is composed of species such as *Kirkia acuminata* and *Afzelia quanzensis* (Table 11). Species of the 4–5 m and >6 m height classes have low percentage canopy spread values in the 0,5 m and 1 m strata (Table 10). In the lower strata, e.g. the 2 m stratum, *Combretum apiculatum*, *Croton gratissimus*, *Hymenocardia ulmoides* and *Diplorhynchus condylocarpon* have high percentage canopy spread values (Table 11).

The largest mean number of individuals per hectare, namely 814 indiv/ha, is found in the 0,5 m height class. In the higher height classes and in the >6 m class only 21 indiv/ha are found. Most of the individuals in the 0,5 m and 1 m height classes are sparse shrubs. Shrubs are relatively scarce except in the 2 m height class (Table 10). Species that occur in relatively high densities in this community are *Monodora junodii* and *Combretum apiculatum* (Table 11) and the species with relatively high percentage apparent canopy covers are *Combretum apiculatum* (8,60 %), *Croton gratissimus* (1,93 %), *Kirkia acuminata* (1,63 %) and *Guibourtia conjugata* (1,61 %) (Table 11).

TABLE 10.
Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv/ha) in different height classes of woody plant species in the *Kirkia acuminata*—*Azelia quanzensis*—*Combretum apiculatum* tree savanna.

Stratum (m)	Percentage canopy spread										Mean number of indiv/ha			
	Total*	Growth form			Height class						Total	Growth form		
		Tree	Sparse shrub	Shrub	>6 m	4-5 m	3 m	2 m	1 m	0.5 m		Tree	Sparse shrub	Shrub
>6	4,25	3,91	0,34		4,25						21	17	4	
4-5	11,06	4,38	5,79	0,89	2,63	8,43					190	75	97	18
3	14,85	4,06	8,32	2,47	0,98	8,45	5,42				217	59	122	36
2	14,50	3,02	7,38	4,10	0,20	3,53	5,19	5,58			550	197	213	140
1	11,20	2,30	5,44	3,46	0,05	0,75	3,02	5,55	1,83		618	233	318	67
0,5	6,77	1,04	3,46	2,27	0,16	0,16	1,04	2,99	1,38	1,20	814	218	517	79
											2 410	799	1 271	340

*Figures in this column are referred to in the text as "Total percentage canopy spread" values.

TABLE 11.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Kirkia acuminata*-*Azela quanzensis*-*Combretum apiculatum* tree savanna.

Plant species*	p.a.c.	indiv/ha	Percentage canopy spread				
			Stratum (m)				
			>6	4-5	3	2	1
<i>Combretum apiculatum</i>	8,60	263	0,13	5,34	6,35	3,26	0,97
<i>Croton gratusimus</i>	1,93	162	0,05	0,61	1,06	0,85	0,76
<i>Kirkia acuminata</i>	1,63	4	1,62	0,59	0,16	0,02	0,43
<i>Guibourtia conjugata</i>	1,61	47	0,26	0,93	1,16	0,75	0,45
<i>Azela quanzensis</i>	1,59	9	1,43	0,68	0,17	0,04	0,09
<i>Combretum zeyheri</i>	1,34	69	0,07	0,65	0,69	0,46	0,33
<i>Monodora junodii</i>	1,10	415			0,15	0,53	0,78
<i>Hymenocardia ulmoides</i>	1,06	46			0,58	0,84	0,57
<i>Diplorhynchus condylocarpon</i>	1,00	42		0,12	0,46	0,80	0,74
<i>Tricalysia allenii</i>	1,00	60			0,02	0,72	0,83

*Only the ten species with the highest percentage apparent canopy over (p.a.c.).



FIG. 7.

The *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest occurring commonly on sandstone hills.

2.2 The *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest

This dry forest is situated on areas underlain by Waterberg Sandstone, Cave Sandstone and the Malvernian Formation at 355 to 475 m above sea level on moderate to steep (up to 22°) rocky slopes (Figs 1 & 7). The fine to medium-textured sand to sandy clay loam soil is dark red-brown to brown-black. Rocks and stones cover up to 60 % of the soil surface, while the soil depth ranges from 100 to 250 mm. The topsoil is apedal with a loose consistency and has a pH between 4.8 and 8.3. The soil usually has a moderate concentration of soluble salts or is strongly leached in places. Carbonates can be found locally.

Floristic composition

Androstachys johnsonii, which grows up to 10 m high, is by far the most conspicuous species in this forest. *Entandrophragma caudatum*, *Euphorbia confinalis* and *Boscia albitrunca* are also abundant species. Adjacent communities are often sharply demarcated from the dry forest and an ecotone is not always present.

The shrub and sparse shrub components are not well developed. Among the species that reside in this community are *Croton pseudopulchellus*, *Phyllanthus*

reticulatus, *Strophanthus kombe*, *Pouzolzia hypoleuca*, *Euphorbia espinosa*, *Dombeya kirkii*, *Monodora junodii*, *Vitex amboniensis* and *Alchornea laxiflora*.

The herbaceous component has a low cover value and the characteristic herbaceous species are *Sporobolus panicoides*, *Achyranthes sicula*, *Enteropogon macrostachyus*, *Setaria ustilata*, *Leptocarydion vulpiastrum*, *Celosia trigyna*, *Cymbosetaria sagittifolia* and *Selaginella dregei*. The associated species are *Danthoniopsis pruinosa*, *Panicum heterostachyum*, *Cleome monophylla*, *Corchorus longipedunculatus*, *Blainvillea gayana*, *Xerophyta equisetoides* and *X. humilis*.

A number of widespread species include *Commelina benghalensis*, *Pseudobrachiararia deflexa*, *Pupalia lappacea*, *Pellaea viridis*, *P. calomelanos*, *Asparagus setaceus* and *Blepharis maderaspatensis*. The absence of *Panicum maximum* and *Digitaria eriantha* is noteworthy.

Trees in this forest form an almost closed canopy leading to poorly developed shrub and herb layers. Termitaria with species such as *Boscia albitrunca*, *Achyranthes sicula*, *Urochloa mosambicensis*, *Panicum deustum*, *Capparis tomentosa* and *Sansevieria* spp. are occasionally found, mainly on the northeast-facing slopes.

Structure

In Tables 12 and 13 as well as in Figures 9 and 10 the structural analysis of the woody vegetation is set out.

Compared to the other Sandveld communities this dry forest has a unique structure. The total percentage canopy spread increases from the 0.5 m stratum to the 4–5 m stratum, which has the highest value (Table 12). The value for the 4–5 m stratum is only slightly higher than for the >6 m stratum. In the 0.5 m and 1 m strata sparse shrubs have the highest total percentage canopy spread, but from the 2 m to the >6 m strata trees contribute the most to the canopy spread values. *Androstachys johnsonii* has the highest percentage canopy spread in all the strata while *Croton pseudopulchellus* shows high values in the lower strata (Table 13). In the 0.5 m stratum the canopy spread is relatively low.

Densities do not vary much between height classes, the lowest density is found in the 3 m height class and the highest density in the 2 m height class. All in all there are more trees than shrubs and sparse shrubs, although sparse shrubs are more numerous in the lower strata. Shrubs are scarce in all height classes (Table 12).

Species with a relatively high percentage apparent canopy cover and density are *Androstachys johnsonii* (44.12 % and 1 900 indiv/ha) and *Croton pseudopulchellus* (3.7 % and 385 indiv/ha) (Table 13).

3. The Rocky Outcrop community

Hills and inselbergs built up of Cave Sandstone of the Karroo System are

TABLE 13.
Percentage canopy spread in different strata; mean number of individuals per hectare (indiv/ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest.

Plant species*	p.a.c.	indiv/ha	Percentage canopy spread				
			Stratum (m)				
			>6	4-5	3	2	1
<i>Androstachys johnsonii</i>	44,12	1 900	23,50	27,51	20,26	13,78	7,20
<i>Croton pseudopulchellus</i>	3,71	385				1,66	2,49
<i>Entandrophragma caudatum</i>	1,78	22	1,78	0,44	0,02		
<i>Croton gratissimus</i>	1,41	165				0,71	1,07
<i>Combretum apiculatum</i>	1,01	22	0,02	0,23	0,83	0,69	0,14
<i>Boscia albitrunca</i>	0,79	11	0,79	0,55			
<i>Combretum zeyheri</i>	0,77	15	0,72	0,67	0,81		
<i>Cassia abbreviata</i>	0,76	33	0,68	0,20			
<i>Phyllanthus reticulatus</i>	0,64	94				0,45	0,23
<i>Diplorhynchus condylocarpon</i>	0,50	11			0,46	0,50	0,35
							0,22
							0,09

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.).



FIG. 8.

The Rocky Outcrop community on Cave Sandstone of the Karroo System.

found at, e.g. Hutwini, Mashikiri and Mukahanya. These outcrops are characterised by trees such as *Stadmannia oppositifolia* subsp. *rhodesica*, *Steganotaenia araliacea*, *Ficus* spp., *Boscia angustifolia* and *Diospyros lycioides* (Figs 1 & 8).

The physiognomic striking species are:

<i>Ficus ingens</i>	<i>Maerua angolensis</i>
<i>F. soldanella</i>	<i>Ptaeroxylon obliquum</i>
<i>F. tettensis</i>	<i>Gyrocarpus americanus</i>
<i>F. sonderi</i>	<i>Euphorbia tirucalli</i>
<i>Commiphora marlothii</i>	<i>Rothmannia fischeri</i>

Common sparse shrubs and shrubs include:

<i>Antidesma venosum</i>	<i>Croton menyhartii</i>
<i>Hippocratea crenata</i>	<i>Drypetes gerrardii</i>
<i>Urera tenax</i>	<i>Adenium obesum</i> var. <i>multiflorum</i>
<i>Vepris reflexa</i>	<i>Hexalobus monopetalus</i>

Widespread herbaceous species are:

<i>Vahlia capensis</i>	<i>Jatropha messinica</i>
<i>Thunbergia hirta</i>	<i>Danthoniopsis pruinosa</i>
<i>Tephrosia virgata</i>	<i>Gloriosa superba</i>
<i>Ocimum canum</i>	<i>Coleochloa rehmanniana</i>

In Figure 8 the pure form of this community is illustrated. In other areas, as illustrated in Figure 1, the Rocky Outcrop community occurs together with the *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest.

4. The Diabase community

This community occurs in the Punda Milia Sandveld area on fine textured dark to very dark red-brown sandy clay loam to clay soil. It is found on diabasic sills west of Punda Milia at 475 to 520 m above sea level (Fig. 1). The most conspicuous woody species are *Acacia nigrescens*, *Combretum collinum*, *C. zeyheri*, *Dichrostachys cinerea*, *Pterocarpus rotundifolius*, *Bolusanthus speciosus* and *Dombeya rotundifolia*. Conspicuous herbaceous species are *Hyparrhenia rufa*, *Setaria holstii*, *Themeda triandra*, *Setaria sphacelata* and *Heteropogon contortus*.

COMPARISON OF STRUCTURE

Vegetation structure is defined by Dansereau (1951) as the organisation in space of the individuals that form a stand (and by extension a vegetation type or a plant association) and the primary elements of structure are growth form, stratification and coverage. Basically vegetation structure is therefore the distribution of biomass in space (Kershaw, 1964).

In Figures 9 and 10 diagrammatic presentations of the total percentage canopy spread and mean total number of individuals per hectare in the different strata and height classes respectively are given for the Sandveld communities.

In five of the six communities represented in Figure 9 the total percentage canopy spread follows more or less the same pattern. There is an increase from the 0.5 m to the 2 m or 3 m strata and above that stratum there is a progressive and pronounced decrease in the total percentage canopy spread values. Community 2.2 (Fig. 9) however, differs from the other five communities in that its total percentage spread values increase up to the 4–5 m stratum and has a high value for the >6 m stratum also.

Generally there are few individuals per hectare in the higher height classes (Fig. 10). The density of community 2.2 once again reveals a totally different pattern. Here a large number of individuals per hectare are found in the 4–5 m and >6 m height classes.

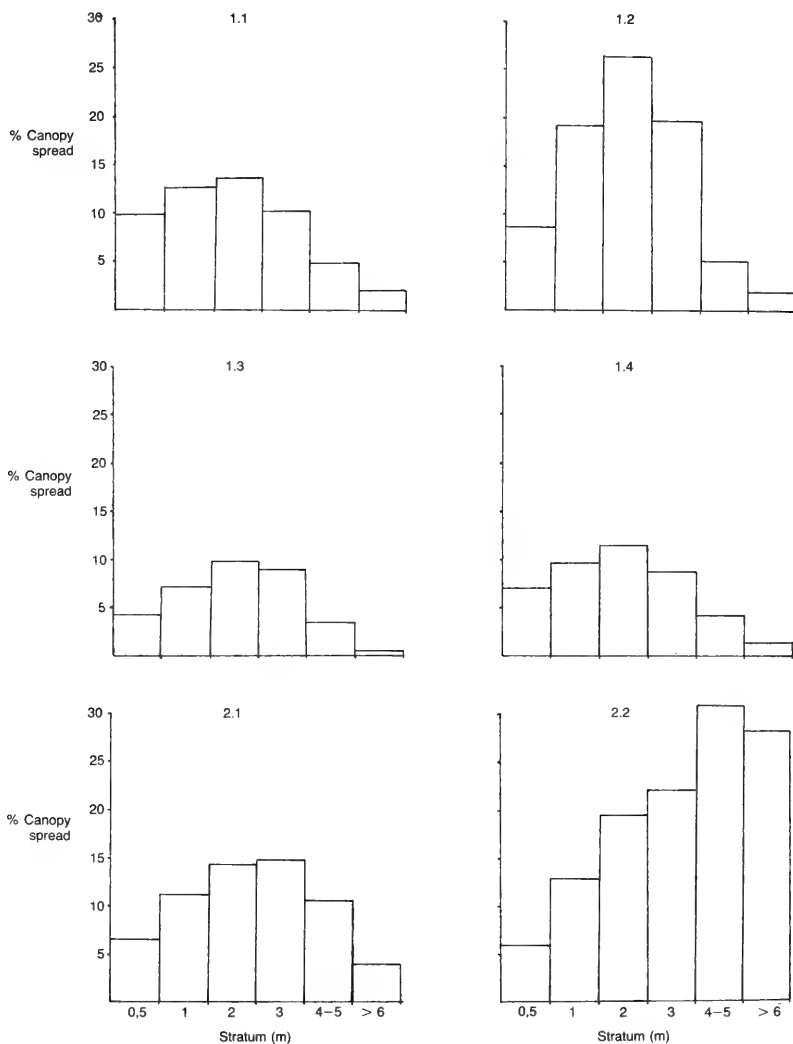


FIG. 9.

A diagrammatic presentation of the total percentage canopy spread in different strata of woody plant species of the Sandveld communities

1.1 The *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna

1.2 The *Baphia massaiensis*—*Guibourtia conjugata* thicket

1.3 The *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna

1.4 The *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna

2.1 The *Kirkia acuminata*—*Azelia quanzensis*—*Combretum apiculatum* tree savanna

2.2 The *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest

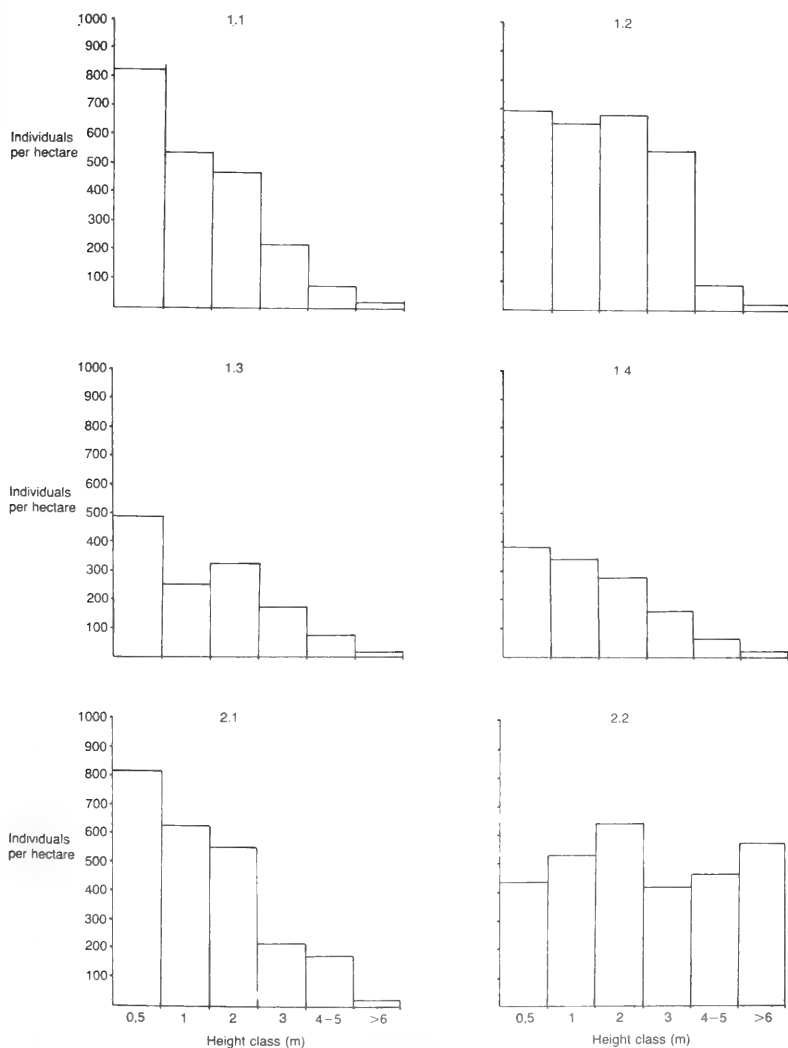


FIG. 10.

A diagrammatic presentation of the mean total individuals per hectare in different height classes of woody plant species in the Sandveld communities

- 1.1 The *Burkea africana*—*Pseudolachnostylis maprouneifolia* tree savanna
- 1.2 The *Baphia massaiensis*—*Guibourtia conjugata* thicket
- 1.3 The *Xeroderris stuhlmannii*—*Combretum apiculatum* tree savanna
- 1.4 The *Terminalia sericea*—*Pogonarthria squarrosa* tree savanna
- 2.1 The *Kirkia acuminata*—*Azelia quanzenis*—*Combretum apiculatum* tree savanna
- 2.2 The *Androstachys johnsonii*—*Croton pseudopulchellus* dry forest

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THE GENUS *AMARANTHUS* IN SOUTHERN AFRICA

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ABSTRACT

A key to and descriptions of the 15 native and introduced species of *Amaranthus* in Southern Africa are given, preceded by a discussion including comments on origins. Some are common weeds. *A. praetermissus* (widely distributed) and *A. dinteri* subsp. *brevipetiolatus* (O.F.S. and Cape Province) are new taxa. *A. dinteri* var. *uncinatus* is transferred to *A. capensis* and a new combination made.

UITTREKSEL

DIE GENUS *AMARANTHUS* IN SUIDELIKE AFRIKA

'n Sleutel tot en 'n beskrywing van die 15 inheemse en ingevoerde soorte van Suidelike Afrika word gegee, voorafgegaan met 'n bespreking van plekke van oorsprong. Sommige is gewone onkruid. *A. praetermissus* (wydverspreid) en *A. dinteri* subsp. *brevipetiolatus* (O.V.S. en Kaapprovinsie) is nuwe taksa. *A. dinteri* var. *uncinatus* word na *A. capensis* oorgeplaas en 'n nuwe kombinasie word gemaak.

Various species of amaranth together provide one of the commonest and most widespread groups of weeds in southern Africa. Almost everywhere, from Cape Town to the tropics, where the ground has been disturbed and there is not too much competition from other vegetation, there will amaranths, often more than one species in company, be found. Only perhaps at high altitudes when the climate is too harsh, are they rare or absent.

Not only do amaranths have an importance to man, albeit usually an unpleasant and unwanted one in their capacity as unwelcome weeds, but some have a more positive economic value. Particularly in the tropics and subtropics, species are cultivated for their edible leafy shoots reminiscent of spinach. In some parts of the world, particularly South America and Asia, the seed is eaten and provides an economic plant product of some local importance. I am not aware that this happens in southern Africa.

In view of their frequency and significance, it seems surprising that apparently only one separate treatment (i.e. not in a check-list or a flora) of *Amaranthus* in southern Africa has so far appeared; that by Adamson in Jl S. Afr. Bot. 2: 191-195 (1936).

The reasons for this comparative neglect are, however, not hard to find. The taxonomy of the genus has been generally recognised as complex, and difficulties and uncertainties abound. Furthermore there is still considerable taxonomic disagreement among experts over important matters. Many species are wide-

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spread and common and have accumulated formidable and complex synonymies, again with uncertainties and disagreements. It is thus difficult or impossible to carry out a satisfactory regional revision without drawing on and assessing knowledge derived from other, widely distant parts of the world. So it is for southern Africa.

In 1961 I published a revision of *Amaranthus* in Britain [Watsonia 4, 6: 261–280 (1961)]. Included here were several species originating from South Africa, some not too well known. During a visit to South Africa at the end of 1975 and in early 1976, special attention was paid to all species of amaranth met with, and this proved most useful in clarifying the concept of various puzzling taxa. As a result it seemed worth-while to try to improve and bring up-to-date the taxonomy of the genus in southern Africa.

The continent of Africa is generally poor in amaranths. The only species almost restricted to tropical Africa is the remarkable *A. sparganiocephalus* Thell., occurring in N.E. tropical Africa and extending to adjacent Arabia. The widespread and variable *A. graecizans* L. may be truly indigenous there, as is *A. thunbergii* Moq. in east tropical Africa, where it occurs northwards to Somalia (in the west to Angola), though this most probably represents a northward extension of range of an originally southern African species.

Southern Africa is thus the most significant part of Africa for the genus. Fifteen species occur, and it is convenient to categorise them into those that are clearly indigenous and those that are not:

A. NATIVE SPECIES

<i>A. thunbergii</i>	South Africa N. to Somalia, Zambia, Angola.
<i>A. dinteri</i>	South, South-West Africa, Botswana.
<i>A. capensis</i>	South Africa and Lesotho.
<i>A. praetermissus</i>	South Africa, South-West Africa, Botswana, Zimbabwe, Angola.
<i>A. schinzianus</i>	South and South-West Africa.

B. PROBABLY OR CERTAINLY NON-NATIVE SPECIES

<i>A. hybridus</i>	Widespread in tropics and subtropics.
<i>A. retroflexus</i>	Native of North America and Mexico.
<i>A. dubius</i>	Native of tropical America.
<i>A. spinosus</i>	Pantropical.
<i>A. blitoides</i>	Native of North America.
<i>A. deflexus</i>	Widespread in tropics and subtropics.
<i>A. lividus</i>	Widespread in tropics and subtropics.
<i>A. viridis</i>	Widespread in tropics and subtropics.
<i>A. standleyanus</i>	Native of Argentina.

It is surprising that the widespread *A. graecizans* L. has apparently not yet been found in the northern part of southern Africa as it is so frequent and widespread in tropical Africa to the north of our area. The comment under several species in category B above that they are widespread should not be taken to imply that that represents their range as native plants. As often happens with widespread weedy species, it may be impossible to separate their original indigenous area from the much larger area they may have subsequently attained as weeds in the footsteps of man.

One cannot help speculating on the possible origin or origins of the indigenous southern African species. The greatest frequency appears to be from the Transvaal and the Orange Free State westwards through the northern part of Cape Province to South-West Africa. At low altitudes in Natal and eastern Cape Province only *A. thunbergii* occurs. All the species, however, occur in the Great Karoo region bounded by Graaff-Reinet, Nelspoort, Prince Albert and Willowmore. All except *A. capensis* reach South-West Africa, but only the widespread *A. thunbergii* occurs in the fynbos regions of the south-western Cape (there are doubtful records of *A. capensis*). The evidence seems to point to a local centre of endemism in the drier parts of south and southern South-West Africa.

As has been already mentioned, tropical Africa is generally poor in native *Amaranthus* species, and the same can be said of Europe and Asia. There is no clear evidence of close affinity between the southern African species and those to the north. It is, however, noteworthy that *Amaranthus* is especially well represented in tropical and South America and with a number of endemic species in Australia.

The native southern African species as a group seem perhaps to be comparable in origin with the South African species of such genera as *Tetragonia*, *Carpobrotus*, and *Cotula*, all of them Southern Hemisphere genera with markedly disjunct distributions in Africa, Australia and South America. It is difficult to achieve any certainty here. The problem has been recently discussed by Goldblatt in Ann. Miss. Bot. Gard. **65**, 2: 369–436 (1974), who (p. 403) suggest the probability of long-distance dispersal. Certainly many species of *Amaranthus*, which usually produce a profusion of seed, have been conspicuously successful in achieving wide ranges.

It would be wrong to give the impression that the taxonomy of *Amaranthus* in southern Africa does not still present a number of problems and uncertainties well worthy of further study. Amaranths are generally not attractive plants to the average collector, especially in South Africa where there are so many more colourful plants to catch the eye. Inadequacy of collected material of some taxa is still an obstacle.

For example, *A. capensis* subsp. *uncinatus* is far better known from adventive material from Europe than as a native in South Africa. Further collections

and study may well cause a revision of its taxonomic status. *A. dinteri* subsp. *brevipetiolatus* might well merit a similar comment.

Amaranthus thunbergii is widely spread both geographically and climatically, and is variable. There may well be ecotypic differentiation and experimental cultivation would certainly be rewarding.

Although a number of hybrids between different species have been recorded in Europe and elsewhere, there has been no clear evidence of hybridisation occurring between the species occurring in southern Africa. Nevertheless, the possibility must be borne in mind.

KEY TO SOUTHERN AFRICAN SPECIES

- la. Axils of stem-leaves mostly bearing paired spines; terminal part of inflorescence spike-like; fruits dehiscent or indehiscent 4. *A. spinosus*
- lb. Axils of leaves without spines:
 - 2a. Inflorescence composed of axillary cymose clusters, the stems thus appearing leafy to apices (Figure 1 B); ♂ and ♀ flowers with 3 perianth-segments (except in 9. *A. praetermissus* and 10. *A. schinzianus*):
 - 3a. Female flowers with 4–5 perianth-segments: leaves oblanceolate to linear:
 - 4a. Perianth-segments of ♀ flowers in fruit spatulate to obovate, not or only very shortly mucronate at apex, 0.75–1.5 (–1.75) mm long, shorter than fruit 10. *A. schinzianus*
 - 4b. Perianth-segments in fruit lanceolate to oblong, ovate-oblong or oblanceolate; acumen at apex variable, often 0.25–1 mm long; the longest ♀ perianth-segments exceeding subequalling or only slightly shorter than fruit:
 - 5a. Leaves not exceeding 10 mm in width; ♀ flowers with subequal perianth-segments with a conspicuous acumen 0.25–1 mm long at apex; widespread native species 9. *A. praetermissus*
 - 5b. Leaves (at least larger stem leaves) usually 10 mm or more wide; ♀ flowers with markedly unequal perianth-segments with only a very short point up to 0.2 mm long at apex; a rare introduction from North America 8. *A. blitoides*
 - 3b. Female flowers always with 3 perianth-segments, variable in shape, but rarely obovate; perianth-segments themselves 1.5–5 mm long; leaves obovate to elliptic:
 - 4a. Perianth-segments equalling or exceeding fruit; fruit circumsessile:
 - 5a. Stems at least when young pubescent with elongate but crisped hairs (hairs sometimes sparse); ♀ perianth-segments narrowed to a fine, suberect or patent, never markedly hooked, subulate acumen 0.75–2 mm long; leaves usually broadest above middle and ± narrowed to the obtuse apex 5. *A. thunbergii*
 - 5b. Stems when young without elongate crisped hairs, but ± clothed with short straight or papilliform hairs; ♀ perianth-segments with a short acumen 0.1–0.5 (0.75) mm long (if longer then acumen conspicuously reflexed-hooked); leaves sometimes as in *A. thunbergii*, but often broadest near the rounded apex:
 - 6a. Female perianth-segments (in fruit) lanceolate, attenuate to a long narrow acumen markedly uncinately hooked above; ♀ perianth-segments 2.5–5 mm long; acumen mostly green with stout midrib. 7. *A. capensis* subsp. *uncinatus*
 - 6b. Female perianth-segments (in fruit) ovate to oblong or ± enlarged or even spatulate above, rounded to shortly nar-

rowed above to an acumen 0,1–0,75 mm long, suberect or spreading, rarely deflexed or \pm hooked; ♀ perianth-segments 0,1–3,5 mm long (rarely to 5 mm):

- 7a. Perianth-segments (at least 1–2) of ♀ flowers strongly broadened above and markedly unequal; apical part of broader segments green with vein-network, obtuse to subacute with a short \pm deflexed mucro about 0,1 mm long; anthers 1 mm long, distinctly exerted from ♂ flowers. 7. *A. capensis* subsp. *capensis*
- 7b. Perianth-segments of ♀ flowers subequal, not or only slightly widened above, mostly ovate to oblong, less markedly venose above, with an erect or \pm spreading point, 0,1–0,75 mm long; anthers about 0,5–1 mm long, only slightly exerted 6. *A. dinteri*
- 4b. Perianth-segments shorter than fruit; fruit indehiscent, leaves nearly always strongly emarginate at apex. 12. *A. lividus*



FIG. 1

A, *Amaranthus hybridus* subsp. *hybridus*. B, *Amaranthus thunbergii*. To show inflorescence-types indicated respectively by alternatives 2b and 2a in the key. A from Scheepers 1279; B from Hanekom 1332.

- 2b. Inflorescence forming a terminal branched or spike-like panicle (Figure 1 A); ♂ and ♀ flowers usually with 5 perianth-segments (3 in *A. deflexus*, *A. lividus* and *A. viridis*):
- 3a. Fruits indehiscent or irregularly rupturing; perianth-segments 3–5:
- 4a. Fruits shorter than, subequalling or scarcely exceeding the ♀ perianth, always strongly and closely rugose or rugose-muricate; ♀ perianth-segments oblong to spatulate, obtuse to rounded, rarely subacute at apex:
- 5a. Leaves linear to linear-lanceolate, rarely lanceolate, not more than 10 mm wide; perennial; ♀ perianth-segments 5 14. *A. muricatus*
- 5b. Leaves ovate to elliptic, mostly more than 10 mm wide; plants usually annual; ♀ perianth-segment 3–5:
- 6a. ♀ flowers with 5 perianth-segments 2–3 mm long; seed very glossy, not or scarcely reticulate, 0.8–1.1 mm in diameter. 15. *A. standleyanus*
- 6b. ♀ flowers with 3 perianth-segments 1–1.5 mm long; seed only slightly shining, with surface minutely and very closely roughened-reticulate. 13. *A. viridis*
- 4b. Fruits distinctly exceeding the ♀ perianth, smooth or only slightly wrinkled on drying; ♀ perianth-segments varying from linear to spatulate and acute to rounded at apex:
- 5a. The fruits ellipsoid, scarcely compressed; seeds ellipsoid; plant perennial; leaves subacute to obtuse and only sometimes slightly emarginate at apex. 11. *A. deflexus*
- 5b. The fruits rotund to shortly pyriform, compressed; seeds ± rounded; plant annual, occasionally a short-lived perennial; leaves nearly always broadly and conspicuously emarginate at apex 12. *A. lividus*
- 3b. Fruits regularly circumscissile; perianth-segments always 5:
- 4a. Stems ± densely clothed with short crisped pubescence, especially above; leaves shortly hairy beneath, especially on midrib and principal nerves; perianth-segments of ♀ flowers with midrib apparently disappearing below the rounded or emarginate apex 2. *A. retroflexus*
- 4b. Stems glabrous to subglabrous or puberulous, sometimes with some short pubescence near inflorescence but then ♀ perianth-segments mostly acute to subacute:
- 5a. Perianth-segments of ♀ flowers mostly acute to subacute, sometimes (subsp. *cruentus*) oblong and subobtusate but not spatulate; bracteoles about as long as to (more usually) twice as long as ♀ flowers 1. *A. hybridus*
- 5b. Perianth-segments of ♀ flowers obtuse to rounded, oblong-spatulate; bracteoles about as long as or only very slightly longer than the ♀ flowers; inflorescence with elongate spiciform branches 20–250 mm long, ♂ towards apex, mixed in middle, ♀ below. 3. *A. dubius*

1. *Amaranthus hybridus* L., Sp. Pl. 990 (1753); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 234 (1914); Adamson in Jl S. Afr. Bot. 2, 4: 192 (1936); Adamson in Adamson & Salter, Fl. Cape Penins. 360 (1950); Henderson & Anderson, Common Weeds S. Afr. 108, figure 53 (1966); Suessenguth & Pod-

lech in Merxmüller, Prodr. Fl. Südwestafr. 33 Amaranthaceae: 8 (1966); Ross, Fl. Natal 158 (1972). Type: grown at Uppsala, Herb. Linnaeus 1117/19 (LINN, lectotype).

Annual. Main stem usually erect, sometimes ascending, 0,15–2,0 (–3,0) m high, subsimple or branched, glabrous to shortly and inconspicuously pubescent especially above. *Leaves* with petiole 10–80 (–150) mm long; axils without spines; lamina variable in shape, elliptic to ovate or lanceolate, 25–150 (–300) mm long, 15–80 (–120) mm wide, glabrous or subglabrous, or slightly and inconspicuously pubescent along midrib and main nerves beneath, attenuate to cuneate towards base, gradually narrowed towards the obtuse to subacute apex, green to red. *Inflorescence* terminal and from upper axils, green, red, purple or yellowish, usually of spiciform branches aggregated into a panicle, sometimes simply spiciform, up to about 500 mm long and 250 mm wide. ♂ and ♀ flowers mixed. *Bracteoles* about as long as to about twice as long as flowers. ♂ *flowers* with 5 ovate-acuminate to oblong-lanceolate perianth-segments 1,5–2,5 mm long. ♀ *flowers* with 5 ovate to oblong perianth-segments 1,5–3,5 mm long, ± aristate-acuminate at apex or the inner acute to subacute or even obtuse; segments usually unequal. *Stigmas* about 0,25–0,75 mm long. *Fruit* about as long as the longer perianth-segments, circumscissile with the upper part swollen and ± wrinkled to not swollen and smooth. *Seed* very glossy, blackish-brown, sometimes white and hardly glossy, rounded-elliptic, 1–1,5 × 0,8–1,25 mm, not or very faintly reticulate.

subsp. **hybridus**; Brenan in Watsonia 4, 6: 267 (1961).

A. paniculatus sensu Cooke & Wright in Thiselton-Dyer, Fl. Cap. 5, 1: 409 (1910); Burt Davy, Fl. Transv. 180 (1926) non L.

A. powellii S. Wats. in Proc. Amer. Acad. 10: 347 (1875); Sauer in Ann. Miss. Bot. Gard. 54, 2: 108 (1967). Type from the U.S.A.

Larger bracteoles of ♀ flowers about 1,5–2 times as long as the perianth. Upper part of fruit (including style-bases) ± inflated and wrinkled, forming a sort of "beak".

S.W.A.—1820 (Tarikora): Omuramba Omatoko, 6 km. NE of Kapupahedi on road to Ndonga (-AB), *de Winter & Marais* 4753 (K), 2017 (Waterberg); Waterberg (-?), *Volk* 1120 (K, PRE).

—2116 (Okahandja); Okahandja (-DD), *Dinter* 311 sub SAM 70761 (SAM).

—2214 (Swakopmund): Haigamkab (Haigamchab) (-DB), *Galpin & Pearson* 7453 sub SAM 1681 (PRE, SAM); Omaruru R. mouth (-AB), *Ihlenfeld, de Winter & Hardy* 3173 (PRE).

—2217 (Windhoek): Windhoek, Aris (-CC), *Seydel* 2587, 3475 (L), 4086 (K).

TRANSVAAL—2330 (Tzaneen): Letaba (-CD), *Scheepers* 643 (K) (untypical with bracteoles shorter than usual).

- 2527 (Rustenburg): Rustenburg (-CA), *Nation* 119 (K).
- 2528 (Pretoria): near Pretoria (-CA), *Wilms* 1251a (BM); Pretoria, the most abundant weed of cultivated ground, *Burt Davy* 885 (BOL); Pretoria, Prinshof Pasture Research Station, *Liebenberg* 3255 (K, PRE); Pretoria, Corellilaan, Les Marais, *Hanekom* 1326 (K, PRE); Pretoria, Division of Botany, *Lansdell* 628 (K); Irene (-CC), *Pole Evans* 4801 (PRE).
- 2530 (Lydenburg): Lydenburg (-AB), *Wilms* 1251 (E, K, PRE); Belfast, Farm Rietvlei (-CA), *Burt Davy* 258, sub Transvaal Dept. Agric. Herb. 3219 (BM).
- 2531 (Komatipoort): Barberton (-CC), *Cotton Exp. Station* 17 (K).
- 2627 (Potchefstroom): Potchefstroom (-CA), *Burt Davy* 1050 (K).
- 2628 (Johannesburg): Johannesburg (-AA), *Moss* 4347 (BM, J).
- 2629 (Bethal): Standerton (-CD), *Burt Davy* 1805 (BOL, K, PRE).
- 2730 (Vryheid): Wakkerstroom (-AC), *Beeton* sub SAM 12442 (SAM).
- O.F.S.—2727 (Kroonstad): Kroonstad (-CA), *Chennell* sub *Rogers* 93 (J, K); about 6 km N of Kroonstad on Johannesburg road, *Scheepers* 1279 (K, PRE).
- 2827 (Winburg): About 15 km W of Winburg by Ventersburg road (-CA), *Brenan* 14096 (K).
- 2926 (Bloemfontein): Bloemfontein, Tempe Farm (-AA) *Potts* 2580 (K); Bloemfontein, Mazels Poort, *Steyn* 43 (NBG); Bloemfontein, O.F.S. Botanic Garden, *Müller* 281 (NBG, PRE); Bloemfontein, O.F.S. Botanic Garden, *Müller* 535 (NBG, PRE).
- SWAZILAND—2631 (Mbabane): Mbabane (-AC), *Nicholson* 17 (K, PRE).
- NATAL—2732 (Ubombo): Lebombo Mountains, Jozini Pass (-AC), *Brenan & Vahrmeijer* 14187 (K, PRE).
- 2830 (Dundee): Wasbank (-AC), *Strey* 8473 (E, K, PRE).
- 2929 (Underberg): Mpendle (Impendhle) (-DB), *Huntley* 482 (PRE).
- 2930 (Pietermaritzburg): Pietermaritzburg (-CB), *Wilms* 2339 (BM, K); Pietermaritzburg, Rushbrook, *de Villiers* 26 (E).
- 2931 (Stanger): Durban Bayhead (-CC), *Ward* 5114, 5116 (K, PRE).
- Grid references unknown: Mooi River (-?), *Johnston* 289 (E); Mooi R., *Medley Wood* 4440 (K); Zululand, Zabamhlofe Res. Station, *West* 722 (L).
- LESOTHO—2828 (Bethlehem): Leribe (-CC), *Dieterlen* 162 (K, PRE, SAM), *Phillips* 516 sub SAM 6292 (SAM).
- 2927 (Maseru): Roma, *Schmitz* 285 (PRE).
- Grid reference unknown: *Cooper* 3048 (K).
- CAPE—2723 (Kuruman): Batlaros (-AC), *Silk* 213 (K, PRE).
- 2824 (Kimberley): Barkley West, Newlands (-DA), *Wilman* sub KMG 3082 (K).
- 2922 (Prieska): Prieska, Golhurt (?) *Bryant* 47 (K).
- 3126 (Queenstown): Queenstown (-DD), *Galpin* 2039 (K), Buffelsfontein (-BC), *Stretton* 208 (PRE).

- 3219 (Wuppertal): Cedarberg, Matjesrivier (-AC), *Wagener* 324, 325 pro parte (NBG).
- 3224 (Graaff-Reinet): Graaff-Reinet (-BC), *Thornton* 202, 203 (K).
- 3226 (Fort Beaufort): Shiloh (-BB), *Baur* 945 (K); Peffers Kop (-DB), *Acoccks* 9749 (L, PRE).
- 3318 (Cape Town): Stellenbosch (-DD), *Duthie* 1460 (BOL); Mowbray (-CD), *Garside* 6159 (BOL); Stellenbosch, Onderpapegaaiberg (-DD), *Taylor* 5651 (K).
- 3319 (Worcester): Karoo Garden, Worcester, weed (-CB), *Brenan* 14045 (K).
- 3321 (Ladysmith): Assegaaibos (-DA), *Fourcade* 5987 (NBG).
- 3323 (Willowmore): Uniondale, Olifants River Warm Baths (-?), *Fourcade* 4957 (K).
- 3325 (Port Elizabeth): Port Elizabeth (-DC), *Laidieu* (?) s.n. (L).
- 3326 (Grahamstown): Grahamstown (-BC), *MacOwan* 3416 sub SAM 153 (SAM); Grahamstown, (-BC), sub GRA 2416 s.n. (K).
- 3327 (Stutterheim): Komga (-DB), *Flanagan* 734, 735 (PRE, SAM).
- 3418 (Simonstown): "Prom. b. spei" (-AD), *Nelson* (BM); Constantia, Bergvliet Farm (-AB), *Purcell* 328 sub SAM 89800 (SAM); Houtbaai (Hout Bay), *Adamson* 807 (BOL); Somerset West (-BB), *Parker* 3470 (BOL, K, NBG).

A. hybridus subsp. *hybridus* is widespread in the tropics and subtropics of the world, usually a weed but sometimes a pioneer in open disturbed ground. It is also a frequent casual in temperate regions, including Europe. It is grown as a grain crop in Asia and America and not infrequently as a decorative plant on account of its red or yellow inflorescence.

A. hybridus subsp. *hybridus* is probably the most widespread amaranth in South Africa, ranging from Cape Town northwards. It is usually a weed of disturbed or cultivated ground and extends from near sea-level to c. 1 800 m. In places it is common—sometimes too common: *Thornton* 202 from Graaff-Reinet notes that it is called "Hells Curse"!

Typical *A. hybridus* subsp. *hybridus* has green inflorescences. However, forms with bright red inflorescences occur which can be called var. *erythrostachys* Moq. in DC., Prodr. 13, 2: 259 (1849). This includes *A. hypochondriacus* L., Sp. Pl. 991 (1753) which Sauer in Ann. Miss. Bot. Gard. 54, 2: 103–137 (1967) regards (in my view unjustifiably) as a distinct species.

Unfortunately the red colour of var. *erythrostachys* Moq. quickly disappears from dried specimens and thus in the absence of notes it may be impossible to identify it with any certainty in the herbarium. From the available field-notes and from personal field observation in South Africa *A. hybridus* subsp. *hybridus*

generally has green inflorescences. But var. *erythrostachys* does occur, though it is clearly uncommon. The certain records are indicated in the citations below. "A. paniculatus L." of Adamson in Adamson & Salter, Fl. Cape Penins.: 360 (1950) may refer to var. *erythrostachys* and is probably based on Adamson 3560 (BOL!) from Rondebosch.

The name *A. caudatus* has been sometimes used on herbarium specimens from South Africa, and occasionally in print, e.g. in Henderson & Anderson, Common Weeds S. Afr. 108 (1966). It is probable that most if not all material named *A. caudatus* in South Africa is referable to *A. hybridus* L. subsp. *hybridus* var. *erythrostachys* Moq. or to *A. hybridus* L. subsp. *cruentus* (L.) Thell. True *A. caudatus* L. is a distinct species often grown in European gardens under the name "Love lies bleeding" and may well occur as a garden plant in South Africa. It is close to *A. hybridus* but has pendulous tail-like red inflorescences and the perianth-segments of the ♀ flowers obovate to broadly spatulate and distinctly imbricate.

The following specimens are those certainly referable to var. *erythrostachys*:

BOTSWANA—2125 (Lothlekane): Lothlekane (-AD), Allen 89 (J, PRE).

TRANSVAAL—2329 (Pietersburg): Pietersburg (-CD), McCallum 137 (PRE); Bandelierkop (-BD), Pole Evans 4804 (42) (PRE).

—2528 (Pretoria): Irene (-CC), Pole Evans 4804 (43) (PRE); Villieria, 27th Ave., 640 (-CA), du Plessis s.n. (PRE); Pretoria (-CA), Kluge 18 (PRE).

—2629 (Bethal); Standerton, Berginsel Farm (-CD), Burt Davy 1805 (PRE).

NATAL—2930 (Pietermaritzburg): Pietermaritzburg, Boulder Hill Game Farm (-CB), Stirton 382 (K).

—3030 (Port Shepstone): Alexandra District, Dumisa, Farm Friedenau (-AD), Rudatis 344 (BM, K).

CAPE—3026 (Aliwal North): Aliwal (-DA), Gerstner 240 (PRE).

—3228 (Butterworth): Kentani (-CB), Pegler 729 (PRE).

—3318 (Cape Town): Rondebosch (-CD), Adamson 3560 (BOL) (Identity probable but doubtful).

—3327 (Peggie): East London (-BB), Ratray 1296 (PRE).

—3527 (Stutterheim): Komga (-DB), Flanagan 735 (PRE).

Indeed typical subsp. *hybridus* is generally remarkably uniform in South Africa, suggesting that it is a comparatively recent introduction, in spite of its frequency and range.

Only two aberrations are worthy of note. Firstly two specimens, one from Natal [-2930 (Pietermaritzburg): Pietermaritzburg, Alexandra Park (-CB), Bot. Dept. Natal University College 101 (K, PRE)] and one from the Transvaal [-2330 (Tzaneen): Tzaneen, Rouman (-CC), Papendorf 397 (PRE)], show the ultimate axes of the flower-clusters (usually so abbreviated as to be scarcely

visible) elongate up to about 5 mm. The main clusters or "spikes" of the inflorescence thus appear to be made up of densely aggregated "spikelets" along which the flowers are closely set. I have seen similar plants from East Africa and they are best regarded for the present as casual abnormalities of subsp. *hybridus**.

Secondly, a few specimens apparently of *A. hybridus* subsp. *hybridus* are abnormally strongly hairy on the stem, petioles and principal vasculature of the leaves beneath. Usually *A. hybridus* is characteristically very weakly hairy, and these more hairy specimens, few in number and scattered in their distribution may represent the products of introgression from *A. retroflexus*. This hybrid is well known in Europe, but not so far from South Africa. Careful observation is needed in the field to clarify the taxonomic status of these specimens, which are as follows:

- CAPE—3128 (Umtata): Nqeleni (-DB), *Strey 11172* (K).
— 3226 (Fort Beaufort): Balfour (-DA), *Moore 22* (PRE).
NATAL—2930 (Pietermaritzburg): Isipingo North (-DD), *Ward 6524* (K, PRE).

In some respects these specimens are also reminiscent of European material named *A. quitensis* H.B.K., a native of S. America very close to *A. hybridus* but with spathulate-obtuse ♀ perianth-segments. As the South African material is in young flower, its possible identity with *A. quitensis* cannot be dismissed.

It is of interest that *A. hybridus* subsp. *hybridus* remains have been recorded (under the name *A. paniculatus* L.) from Scott's Cave, a Later Stone Age site in the Gamtoos Valley WNW. of Port Elizabeth [M. J. Wells in S. Afr. Arch. Bull. 20, 78 (2): 80–84 (1965)]. The cave was probably occupied between 1500 and 1790 A.D., before European penetration of the area, though an introduced amaranth may well have reached the area beforehand. At least this discovery is testimony to the relative antiquity of *A. hybridus*, even as a weed, in South Africa.

* Further material of this taxon from elsewhere has recently become available: Zimbabwe, cult. at Salisbury, *VS 118*, *VS 110*; India, Khasra, Chotandaipur, 16 Oct. 1969, *D. N. Thakur DNT 512*. Its peculiarities are maintained, but its taxonomic position made even more puzzling. The inflorescences are very long and tail-like, up to about 550 mm, interrupted below. The elongate bracteoles much exceed the flowers (cf. *A. albus* L.). The ♀ perianth-segments in the mature Indian specimen become obovate, rounded and minutely apiculate at apex, and white except for the green midrib. There is here some resemblance to *A. retroflexus*, but the inflorescences, both whole and partial are very different, and the indumentum of *A. retroflexus* is lacking. More material and observation are much needed.

subsp. *cruentus* (L.) Thell., Fl. Adv. Montpellier 205 (1912); C. C. Townsend in Nasir & Ali, Fl. W. Pakistan 71: 12 (1974) & in Publ. Cairo Univ. Herb. 7-8: 64-66 (1977).

A. cruentus L., Syst. Nat., ed. 10, 1269 (1759); Sauer in Ann. Miss. Bot. Gard. 37: 601, fig. 5 (p. 598) (1950); Henderson & Anderson, Common Weeds S. Afr. 108 (1966); Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwest-afr. 33 Amaranthaceae: 7 (1966). Type: Herb. Linnaeus 1117/25 (LINN, lecto-type).

Larger bracteoles of ♀ flowers about as long as to $1\frac{1}{2}$ times as long as the perianth. Upper part of fruit (including style-bases) short, firm, not "beaked" inflated or wrinkled.

BOTSWANA—N:—1922 (Nokaneng): Mutsoi, NE of Nokaneng (-CA), *Lambrecht 110* (K); N: Thaoge R. bank at Sehlabakgetse, 19° 24'S, 22° 11.3'E, *Smith 1695* (K).

SE:—2425 (Gaborone): Gaborone campus (-DB), *Mott 179d* (K); Gaborone, Broadhurst, *Hansen 3095* (K).

TRANSVAAL—2330 (Tzaneen): Modjadjis near Duivelskloof (-CB), *Krige 170* (PRE); by road en route to Politsi (-CC), *Scheepers 267* (K); roadside Levubu—Albasini Dam (-AB), *Brenan 14174* (K, NBG, PRE).

—2628 (Johannesburg): Johannesburg, Milner Park (-AA), *Moss 6676* (J).

NATAL—2930 (Pietermaritzburg): Isipingo Beach (-DD), *Ward 6533* (PRE).

—2931 (Stanger): Durban, Bayhead (-?), *Ward 5119* (PRE).

The taxonomy of *A. hybridus* presents considerable problems. Thellung in his fine account of the genus in Ascherson and Graebner's *Synopsis der Mitteleuropäischen Flora* 5, 1 (1914) adopted a "wide" view of the limits of the species, which I followed in my account of the British species in *Watsonia* 4, 6: 267-269 (1961). However, Sauer in his valuable account of the grain amaranths and their relatives in Ann. Miss. Bot. Gard. 54, 2: 103-137 (1967) put forward a very different opinion, recognising as distinct four species that had been amalgamated in Thellung's account: *A. hybridus* L., *A. powellii* S. Wats. in Proc. Amer. Acad. 10: 347 (1875), *A. hypochondriacus* L. and *A. cruentus* L. There is no doubt that the four species as defined by Sauer encompass a wide range of plants often with spectacular differences of colour, size and form and that these are frequently genetically controlled.

The problem has been recently carefully and critically reassessed by Townsend in Publ. Cairo Herb. 7-8: 64-66 (1977) and I have re-examined the wide range of material myself. I can only follow Townsend in maintaining a "wide" concept of *A. hybridus* and I accept his verdict that what I called in 1961 *A. hybridus* subsp. *incurvatus* (Timeroy ex Gren. and Godr.) Brenan should cor-

rectly be subsp. *cruentus*. I am very grateful to Mr C. C. Townsend for help and advice on this complex matter.

2. *Amaranthus retroflexus* L., Sp. Pl. 991 (1753); Cooke & Wright in Thiselton-Dyer, Fl. Cap. 5, 1: 410 (1910); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 254 (1914); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 485, t.95, fig. 5, 5a, c-e, fig. 209 (p. 470), fig. 241 (p. 486), fig. 242 l-r (p. 505) (1959); Brenan in Watsonia 4, 6: 270 (1961). Type: cultivated at Uppsala, Herb. Linnaeus 1117/22 (LINN, lectotype).

Annual. Main stem erect, usually with ascending branches, up to about 1 m high, but often much less, \pm densely clothed with short crisped pubescence, especially above. *Leaves* with petioles mostly long, 15–80 mm long; axils without spines; lamina ovate to elliptic or oblong-ovate, often slightly rhombic, mostly 30–90 (–150) mm long, 15–40 (–65) mm wide, shortly hairy especially on midrib and main nerves beneath, much less so above, cuneate-attenuate at base, obtuse to subacute at apex, sometimes slightly emarginate and mucronate as well, green and without darker blotches. *Inflorescence* greenish-white, of dense rather thick terminal and axillary spikes which are themselves usually shortly branched, the spikes thus lobed and forming dense terminal and axillary panicles; elongate cylindrical spiciform branches absent. *Bracteoles* subequalling to twice as long as the flowers. σ flowers few, mainly towards ends of branches, with 5 oblong-elliptic perianth-segments. f flowers with 5 oblong-spathulate to spathulate perianth-segments about 1.75–2.75 mm long, whitish with green midrib becoming colourless and apparently disappearing below the rounded or emarginate and often mucronate apex. *Stigmas* 0.5–0.75 mm long. *Fruit* shorter than the perianth, circumscissile, smooth. *Seed* very glossy, blackish-brown, 1–1.25 mm in diameter; surface smooth or very faintly reticulate, not at all verrucose.

var. *retroflexus*; Brenan in Watsonia 4, 6: 270 (1961).

Longer bracteoles of f flowers about twice as long as the flowers.

NATAL—2930 (Pietermaritzburg): Durban, Merebank Central (-DD), *Baijnath* 224 (PRE).

CAPE—2824 (Kimberley): Kimberley, garden (-DB), *Bunting* sub McGregor Museum, Kimberley 1365 (BOL, K).

—3225 (Somerset East): Boschberg (-DC?), *MacOwan* 1957 (K).

var. *delilei* (Richter & Loret) Thell. in Vierteljahrsschr. N. G. Zürich 52: 442 (1907); Thell. in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 260 (1914); Aellen

in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 486 (1959); Brenan in *Watsonia* 4, 6: 271 (1961). Type from France.

Longer bracteoles of ♀ flowers about $1\frac{1}{3}$ – $1\frac{1}{2}$ as long as the flowers.

CAPE—3226 (Fort Beaufort): Shiloh (-BB), *Baur 1139* (K).

Native of North America and extending southwards to Mexico. An introduction in many parts of the world including Europe, North Africa, temperate Asia from Cyprus and Turkey to China and Japan, Australia, South America and South Africa. Occurs in more temperate regions than a number of related species.

A. retroflexus is very variable in size. Starved specimens in poor ground may flower and fruit when only a small number of millimetres high, but there is no evidence for regarding this variation as anything but phenotypic.

It is usually easily identified by its paniculate terminal as well as lateral inflorescence with a shortly lobed outline but without elongate tail-like branches, densely pubescent stems, female flowers with 5 spathulate perianth-segments, and by the circumscissile fruits.

3. *Amaranthus dubius* Mart. ex Thell., Fl. Adv. Montpellier 203 (1912); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 265 (1914); Aellen in Hegi, Ill. Fl. Mitteleur. ed. 2, 3, 2: 476, fig. 201 (p. 468) (1959). Type from tropical America.

Annual. Main stem erect, up to about (0,15–)0,3–1(–2) m high, with numerous branches, glabrous, or with some short pubescence near the inflorescence. *Leaves* with petiole very variable in length, but usually some, especially on main stems, long, 30–90 (sometimes –140) mm long; axils without spines; lamina usually ovate to elliptic, often somewhat rhombic, mostly 20–120 (sometimes –190) mm long, 13–70 (sometimes –125) mm wide, glabrous or subglabrous, attenuate at base itself but immediately above usually widening and rounded or broadly cuneate, obtuse or sometimes rounded and minutely mucronate and often slightly emarginate at apex, green and without darker blotches. *Inflorescence* a green, ± branched terminal panicle with leafless spiciform branches 20–180(–250) mm long, below often interrupted with ± numerous axillary flower-clusters; terminal parts of branches either with ♂ cymules or with ♂ and ♀ flowers mixed; middle part of branches often with cymules with both ♂ and ♀; basal part wholly or predominantly ♀. *Bracteoles* about as long as or slightly longer than the flowers. ♂ *flowers* with 5 ovate-subacuminate perianth-segments. ♀ *flowers* with 5 oblong-spathulate perianth-segments about 1,5–2,5 mm long, whitish with green midrib, rounded and often very shortly mucronate at apex. *Stigmas* 0,5–1,0 mm long. *Fruit* about as long as or slightly shorter than the perianth, circumscissile, not closely and regularly rugose. *Seed* very glossy,

chestnut-black, 0.8–1 mm in diameter; surface very faintly reticulate, almost smooth, the areolae slightly smaller in comparison with the mesh.

Native of tropical America. Widespread but introduced in tropical Africa. Occasionally adventive in Europe (Aellen, 1959).

NATAL—2930 (Pietermaritzburg): Durban Merebank East (-DD), Ward 5385 (PRE); Isipingo North, Ward 6523 (K, PRE).

—2931 (Stanger): Inanda, Tongaat (-CA), Ramasamy 27 (PRE); Durban (-CC), Ward 5117 (K, PRE).

CAPE—3129 (Port St. Johns): Port St. Johns (-DA), Moss 4348 p.p. (BM, J).

As Thellung (1914) pointed out, *A. dubius* is most closely related to *A. spinosus*, differing in the constant absence of axillary spines as well as in other characters. Although not a constant difference, and with some degree of overlap, the leaves of *A. dubius* are usually broader and generally ovate rather than lanceolate in outline; the ♀ perianth-segments have often wider white margins and are more rounded and less mucronate at apex; the stigmas are also shorter. Hybrids between the two have been reported (see Thellung, 1914), though not from South Africa; they are apparently rare and as *A. dubius* is the only known polyploid species of *Amaranthus* (see Sauer, 1967) likely to be largely sterile.

Sauer in *Ann. Miss. Bot. Gard.* **54**: 106 (1967) keyed out *A. dubius* and *A. spinosus* by the distribution of the ♂ and ♀ flowers, as well as by the presence or absence of spines. He stated that *A. spinosus* has the lower cymules ♀, the upper ♂, while *A. dubius* has each cyme with a terminal ♂ flower and the rest ♀. The statement is true for *A. spinosus*, but the distribution of the sexes in *A. dubius* is much less constant, sometimes as was described by Sauer but sometimes barely distinguishable from *A. spinosus*. Generally, however, there is a greater tendency for cymules of mixed sex in *A. dubius*.

4. *Amaranthus spinosus* L., Sp. Pl. 991 (1753); Cooke & Wright in Thiselton-Dyer, Fl. Cap. **5**, 1: 409 (1910); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. **5**, 1:267 (1914); Burtt Davy, Fl. Transv. 180 (1926); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, **3**, 2: 477, fig. 202 (p. 468) (1959); Brenan in Watsonia **4**, 6: 271 (1961); Henderson & Anderson, Common Weeds S. Afr. 110, fig. 54 (1966); Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr., 33 *Amaranthaceae*: 9 (1966); Ross, Fl. Natal 158 (1972). Type cultivated at Uppsala, Herb. Linnaeus 1117/27 (LINN, lectotype).

Annual. Main stem erect, up to about 0.3–1.5 m high, with numerous branches, glabrous, or with some short pubescence near the inflorescence. *Leaves* with petiole very variable in length, but usually some, especially on main stems. long, 30–70 (–90) mm; axils nearly always with 2(–4) divaricate spines about

5–15 (–25) mm long, green with straw-coloured tip; lamina ovate to lanceolate or oblong, often somewhat rhombic, 20–80 mm long, 7–30 mm wide, glabrous or subglabrous, attenuate at base, obtuse or slightly emarginate and minutely mucronate at apex, green and without darker blotches. *Inflorescence* a green, \pm branched terminal panicle with leafless spiciform branches 20–150 mm long, below interrupted with \pm numerous axillary flower-clusters; terminal parts of branches with σ cymes, lower and axillary cymes φ , the latter often with spines. *Bracteoles* rather shorter than to about as long as flowers. σ flowers with 5 ovate-subacuminate perianth-segments. φ flowers with 5 oblong-spathulate perianth-segments about 1–2,5 mm long, whitish with green midrib, rounded to sometimes subacute and very shortly mucronate at apex. *Fruit* about as long as or shorter than the perianth, not closely and regularly rugose; lid clearly defined but often not opening. *Stigmas* 0,75–1,5 mm long. *Seed* very glossy, deep, chestnut-brown to blackish, about 0,7–1 mm in diameter; surface smooth or only slightly roughened, not closely and regularly reticulate.

A pantropical weed, probably originating in tropical America.

BOTSWANA—N:—1824 (Kachikau): Kachikau (-AB), *Munro ML 10* (K, PRE).

—N:—1923 (Maun): Maun (-CD), *Lambrecht 238* (K, PRE).

—SE:—2425 (Gaborone): Gaborone, The Mall, *Hansen 3421* (PRE).

—2426 (Mochudi): Mochudi, Phutodikobo Hill (-AC), *Naomi Mitchison 68* (K).

S.W.A.—2116 (Okahandja): Okahandja, Farm Quickborn (-DD), *Bradfield 420* (PRE).

—2217 (Windhoek): Windhoek (-CA), *Giess 10551* (PRE).

TRANSVAAL—2330 (Tzaneen): Duiwelskloof (-CA), *Davidson 1/75* (NBG); Letaba (-CD), *Scheepers 644* (K, PRE).

—2430 (Pilgrim's Rest): Shiluvane (-AB), *Junod 1062* (K).

—2526 (Zeerust): Zeerust (-CA), *Pott 4347* sub SAM 9503 (SAM).

—2527 (Rustenburg): Rustenburg (-CA), *Nation 122* (BOL, K).

—2528 (Pretoria): Pretoria (-CA), *Leendertz 7* (K, PRE), *Burt Davy 1072* (K, PRE); Pretoria, Corellilaan, Les Marais, *Hanekom 1325* (K).

—2530 (Lydenburg): Waterval Boven (-CB), *Burt Davy 1548* (K, PRE); Lowveld Botanic Garden (-BD), *van Jaarsveld 245* (NBG, PRE).

—2531 (Komatiipoort): Barberton (-CC), *Burt Davy 300* (BOL, PRE).

Grid reference unknown: The Downs (?), *Moss & Rogers 267* (BM).

NATAL—2829 (Harrismith): Winterton (-DC), *Harding 843* (K).

—2930 (Pietermaritzburg): Camperdown, Nagle Dam (-DA), *Wells 1120* (E, K); Durban, N end of Berea Ridge (-DD), *Galpin s.n.* (NBG), *Galpin 12102* (K, PRE).

—2931 (Stanger): near Durban (-DD), *Medley Wood 1762* (BOL, K), *Wilms 22381* (BM, K, PRE) (BM sheet 22381), *Theron 805* (K, PRE); Durban, Bluff (-CC), *Pillans* sub SAM 16556 (SAM).

—3030 (Port Shepstone): Ixopo (-AA), *Schlechter 6679* (K).

CAPE—3129 (Port St. Johns): Port St. Johns (-DA), *Mogg 13147* (K, PRE).

A. spinosus is very easily recognised from all other species in the genus by the presence of obvious axillary spines. Although Thellung (1914) mentions unarmed or almost unarmed variants, such have not been found in South Africa and are anyhow more likely to be hybrids between *A. spinosus* and *A. dubius* (see also Sauer, 1967). For the differences between these two species, see under *A. dubius* (p. 464).

5. *Amaranthus thunbergii* Moq. in DC., Prodr. **13**, 2: 262 (1849); Cooke & Wright in Thiselton-Dyer, Fl. Cap. **5**, 1: 410 (1910) pro max. parte, excl. *Baur 971* & verisim. *Burt Davy 1802*; Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. **5**, 1: 280 (1914); Burt Davy, Fl. Transv. 181 (1926); Adamson in Jl S. Afr. Bot. **2**, 4: 193 (1936); Adamson in Adamson & Salter, Fl. Cape Penins. 361 (1950); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, **3**, 2: 496, fig. 223 (p. 471) (1959); Brenan in Watsonia **4**, 6: 271 (1961); Henderson & Anderson, Common Weeds S. Afr. 112, fig. 55 (1966); Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr., 33 Amaranthaceae: 8 (1966), pro parte—vide *A. praetermissum*; Ross, Fl. Natal 158 (1972). Type (see notes below, p. 470): South Africa, Herb. Thunberg negative No. 933, exposure No. 6 (VRS, isosyntype).

Annual. Stems decumbent or erect, 70 mm to 1 m high, \pm branched especially below but sometimes throughout, when young \pm pubescent (sometimes sparsely) with crisped elongate hairs. Leaves with petiole 3–40 mm long, variable in length on a single plant; axils without spines; lamina obovate-elliptic to obovate or rarely oblanceolate, sometimes almost elliptic, mostly 10–16 mm long, 5–30 mm. wide, glabrous or subglabrous, attenuate or cuneate-attenuate at base, often \pm narrowed above to an obtuse or rounded or sometimes slightly emarginate apex, sometimes rounded above, green or sometimes with a purplish central blotch. Inflorescence of dense axillary clusters extending to near base of stem, clusters often confluent above; inflorescence leafy throughout. Bracteoles lanceolate, shorter than perianth. σ^7 flowers with 3 ovate-elliptic perianth-segments with a conspicuous awn-like spreading or somewhat curved outwards (but not uncinat) point 0.5–1 mm long; anthers exserted, 1.5 mm long. f flowers with (in fruit) 3 unequal, ovate-oblong to lanceolate perianth-segments 3–5 mm long, with greenish midrib usually not or scarcely branched above and not or slightly thickened, gradually acute at apex and narrowed to a fine suberect or \pm spreading awn-like point 0.75–2 mm long. Stigmas 0.75–1 mm long. Fruit ellipsoid-ovoid, shorter than perianth, circumscissile, smooth or slightly rugose

above. *Seed* ellipsoid-rounded, glossy, blackish, 1–1.25 mm in diameter, minutely roughened and very finely impressed-reticulate on surface.

A. thunbergii is rather widespread in Africa, from South Africa northwards through East Africa to Uganda and Somalia, in the west extending to Zambia and Angola.

BOTSWANA—N:—2124 (Rakops): Botletle R., Toromoja (-BA), *Sampson* 57 (K), *Ngoni* 436 (K, PRE); N: Boteti R. and Samedupe Bridge, 20° 06.7' S., 23° 31.6' E., *Smith* 1840 (K); N: Lake Ngami, 20° 26' S., 22° 59.75' E., *Smith* 1919 (K, PRE).

SW:—2121 (Ghanzi): Ghanzi (-DA), *Brown s.n.* (K).

SW:—2622 (Tsabong): Ditatso Pan 40 km. N.W. of Tsabong (-AB), *Leistner* 3061 (EAH, PRE).

SE:—2425 (Gaborone): Gaborone campus (-DB), *Mott* 827 (K, PRE).

—2426 (Mochudi): Mochudi (-AC), *Harbor* sub *Rogers* 6442 (J, K).

S.W.A.—1715 (Ondangua): E of Oshikango (-BD), *Rodin* 9049 (K, PRE).

—1719 (Runtu): Kapako Camp E of Mupini (-DC), *de Winter & Marais* 4499 (K).

—1813 (Ohopoho): Kaoko Otavi (-BC), *de Winter & Leistner* 5589 (K).

—2016 (Otjiwarongo): Omatjenne (-AD), *Volk* 2939 (K).

—2116 (Okahandja): Okahandja (-DD), *Dinter* 147 sub SAM 70760 (SAM).

—2214 (Swakopmund): Haikamchab (-DB), *Galpin & Pearson* 7453 (K).

—2818 (Warmbad): Sandfontein (-DA), *Wilman s.n.* (K).

Grid reference uncertain: W of Kalkfontein, *Range* 1390 sub SAM 70763 (SAM).

TRANSVAAL—2330 (Messina): Messina (-AC), *Rogers* 20853 (J).

—2430 (Pilgrim's Rest): Sekhukuniland, Driekop (-CA), *Mogg & Barnard* 607 (K, PRE).

—2528 (Pretoria): Pretoria (-CA), *Leendertz* 10413 (K, PRE); Pretoria, Corellilaan, Les Marais, *Hanekom* 1332 (K, PRE).

—2531 (Komatipoort): Barberton (-CC), *Rogers* 18356 (K), *Cotton Exp. Station* 27 (K).

—2627 (Potchefstroom): Potchefstroom Farm (-CA), *Burt Davy* 1051 (BOL, K, PRE), 1057 (K).

—2628 (Johannesburg): Johannesburg, Forest Town (-AA), *Moss* 9321 (BM, J); Pretoria, Birchleigh, *Moss* 14402 (BM, J).

—2725 (Bloemhof): Schweizer Reneke, Vierfontein (-AB), *Burt Davy* 1683 (PRE); Bloemhof, S.A. Lombard Nature Reserve (-DA), *Leistner* 47 (K).

Grid references unknown: Marico District, *Holub s.n.* (K); Springbok Flats, *Burt Davy* 1740 (K, PRE); "P.P. Rust", *Leendertz* 1939 (K).

O.F.S.—2827 (Winburg): 15 km. W of Winburg on Ventersburg road (-CA), *Brenan* 14097 (K, PRE), *Brenan* 14098 (K).

- 2926 (Bloemfontein): Bloemfontein (-AA), *Potts* 635 (L).
 SWAZILAND—2531 (Komatipoort): Tshaneni (-DC), *Barrett* 199 (PRE).
 NATAL—2732 (Ubombo): Sordwana Bay (-DA), *Brenan & Vahrmeijer* 14227 (K, PRE).
 —2832 (Mtubatuba): Hlabisa District, Hluhluwe Game Reserve (-AA), *Ward* 4780 (K, PRE).
 —2929 (Underberg): Tabamhlope (-BA), *West* 982 (K, PRE).
 —2930 (Pietermaritzburg): Inanda (-DB), *Wood s.n.* (K).
 LESOTHO—2828 (Bethlehem): Leribe (-CC), *Dieterlen* 524, 995 (K, PRE, SAM).
 —2927 (Maseru): Roma, University Campus (-BC), *Schmitz* 1467, 6347 (PRE).
 Grid references unknown: *Cooper* 186 (K), 3049 (K).
 CAPE—2624 (Vryburg): Vryburg, Armoedsvlakte (-DC), *Mogg* 8243 (L).
 —2723 (Kuruman): Takoon (-BB), *Burchell* "ex S 212 Cat. Geogr. 2221-2" (K); Albert District (-BC), *Cooper* 789 (E (p.p.)), (mixed with *A. capensis*).
 —2824 (Kimberley): Kimberley (-DD), *Moran s.n.* p.p. (NBG), *Wilman s.n.* (K); Witpan (-?), *Wilman s.n.* (K).
 —3022 (Carnarvon): Krantzfontein (-BC), *Wilman s.n.* (K).
 —3123 (Victoria West): Murraysburg (-DD), *Tyson* 51 p.p., sub SAM 43406 (SAM).
 —3318 (Cape Town): Cape Town (-CD), *Herb. A. Prior s.n.* (K); Claremont *Schlechter* 275 (BM, PRE), 278 (K); Groote Schuur (-CD), *Wolley Dod* 1142 (BM, BOL, K); Rondebosch, *Adamson* 2357 (BOL); Rondebosch, Sandown Road, *Wolley Dod* 2483 (BM); Stellenbosch (-DD), *Moss* 4349 (BM, J); Jonkershoek, *Parker* 4559 (K, NBG).
 —3322 (Oudtshoorn): Farm Doornkraal de Rust (-?), *Dahlstrand* 2455 (J, PRE).
 —3224 (Graaff-Reinet): Graaff-Reinet (-BC), *MacOwan* 357 (K), *Bolus* 357 (BOL, K, PRE).
 —3324 (Steytlerville): Uitenhage, near the Zwartkopsrivier (-DB), *Zeyher* 576 (BM, BOL, K, NBG, PRE, SAM), *Zeyher* 3611 (NBG, SAM).
 —3325 (Port Elizabeth): Uitenhage (-CD), *Herb. A. Prior s.n.* (K).
 —3326 (Grahamstown): Grahamstown (-BC), *Glass* 360 (NBG).
 —3418 (Simonstown): Cape Town, between Lakeside and Poll's Moor, E end of Westlake Golf Course (-AB), *Brenan* 14023A (K, MO, NBG, PRE); Bergvliet Farm, Constantia, *Purcell s.n.* (SAM); "Promont. b. spei" (-AD), *B.S.* 1771 (BM); Somerset West (-BB), *Parker* 3480 (BOL, K, NBG); Cape Peninsula, Edinburgh Estate, bed of Liesbeck R. (-?), *Salter* 9012 (BOL).
 Grid references unknown: *Drège s.n.* (BM, E, K), *Ecklon & Zeyher* 2, 3 (K), *Fraser s.n.* (E), *Scott Elliot* 662 (E); "C.B.S.", *Pappe s.n.* (K); "In ruderalis hortis ubique", *Pappe* sub SAM 19200 (SAM).

According to a letter dated 17 October 1913 from Thellung to Stapf, preserved in the Kew Herbarium, a search of likely herbaria had failed to reveal any authentic material of *A. thunbergii*, except for a sheet of Zeyher 576 in Hooker's herbarium at Kew annotated as *A. thunbergii* in Moquin's own hand.

Moquin (*l.c.*) based the species on material from "Ad caput Bonae-spei (Thunb. herb. Hook.! Krauss!)". There is no Thunberg specimen in the Hooker Herbarium at Kew, and it seems at least possible that three entities are meant in Moquin's citation, though it seems puzzling that there is no exclamation-mark after "Thunb.", and perhaps it was omitted in error.

I am much indebted to Mr C. C. Townsend for information and advice here, and am content to follow his opinion that the specimen in Thunberg's own herbarium at Lund (IDC microfiche, negative No. 933, exposure No. 6), whose identity is beyond doubt, might be reasonably accepted as an isosyntype of the species.

Usually *A. thunbergii* is readily separable from *A. dinteri* by the presence of long hairs (sometimes sparse) on the young stems at least, the leaves usually more narrowed towards apex, and the fine awn-like part to the ♀ perianth-segments mostly 1 mm long or more in fruit. In addition the segments generally appear whitish with a green midrib, usually lacking the network of branched green venation in the upper part so often seen in *A. dinteri*.

Occasionally plants occur referable in my view to *A. thunbergii* but showing trends towards *A. dinteri*. For example Volk 2939 and de Winter & Leistner 5589 (South-West Africa) and Leendertz 10413 (Pretoria) are typical *A. thunbergii* except for the midrib of the ♀ perianth-segments being more thickened above and sometimes with an expanded area of green venation. An unnumbered Wilman specimen (Prieska, Mar. 1934) shows similar trends and is almost glabrous even on the young stems. A specimen at Kew (Herb. Prior *s.n.*, Cape Town) is similar to *A. thunbergii* except for the short awns (mostly 0.5–0.75 mm long, sometimes 1 mm).

A. thunbergii and *A. dinteri* are usually quite distinct from one another, but these occasional perplexing plants occur. Their taxonomic status is not certain, but it seems at present advisable to keep the two species distinct, but to admit the possibility of occasional hybridisation, as happens not infrequently elsewhere in the genus.

6. *Amaranthus dinteri* Schinz in Mém. Herb. Boiss. **20**: 15 (1900); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. **5**, 1: 295 (1914); Adamson in JI S. Afr. Bot. **2**, 4: 193 (1936); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, **3**, 2: 502 (1959); Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr. **33** Amaranthaceae: 7 (1966). Type: South-West Africa, Salem, *Dinter* 129 (Z, holotype).

Annual. Stems decumbent or erect, about 100–400 mm long, usually much branched especially below, subglabrous when young or ± puberulous with short

straight or papilliform hairs, without pubescence of crisped elongate hairs. *Leaves* with petiole mostly 3–15 (–20) mm long, variable in length; axils without spines; lamina obovate to obovate-elliptic, mostly 5–25 (sometimes –30) mm long, 3–13 (sometimes –18) mm wide, glabrous or subglabrous, attenuate at base, obtuse to rounded and minutely mucronate and sometimes slightly emarginate at apex, wholly green or sometimes with a purplish central blotch. *Inflorescence* of dense axillary clusters extending to near base of stem; clusters often confluent above; inflorescence thus leafy throughout. *Bracteoles* lanceolate, shorter than perianth, often curved outwards or downwards. ♂ *flowers* with 3 elliptic to lanceolate, shortly acuminate perianth-segments; *anthers* only shortly exerted from flower, 0.5–1 mm long. ♀ *flowers* with 3 ovate to oblong perianth-segments 1.5–3.5 mm long, whitish with green midrib and often some venation above, acute or sometimes obtuse at apex, but mostly narrowed to a suberect or spreading acumen 0.1–0.5 (–0.75) mm long. *Stigmas* 0.5–0.75 mm long. *Fruit* ovoid to nearly round, shorter than to subequalling perianth, circumscissile, \pm coarsely rugose above. *Seed* glossy, black or brownish-black, 1–1.5 mm in diameter; surface faintly reticulate and very finely roughened.

A. dinteri is restricted to South and South-West Africa, but occasionally introduced in Europe.

subsp. *dinteri*

Internodes variable in length, but those on the principal stems at least often comparatively long, 10–13 mm in length. Petiole variable but some at least 7–15 (–20) mm long. Leaf-lamina often 10–25 sometimes to 30 mm long.

The length of the female perianth-segments in subsp. *dinteri* is decidedly variable. The available material can be sorted into two groups which I provisionally call var. 'A' and var. 'B'. The great majority of specimens fall under 'A'. The taxonomic status of these two groups is very uncertain and needs further study in the field and cultivation and for that reason it seems wise not to give them formal recognition by names until their status has been more clarified.

Through the kindness of the Director of the Botanischer Garten und Museum der Universität Zürich, I have received on loan the type of *A. dinteri*, *Dinter 129*, a poor, stunted, apparently grazed specimen, but clearly belonging to the species as customarily understood and coming under var. 'A'.

var. 'A.'

Female perianth-segments in fruit 1.5–2.5 mm long, with acumen 0.1–0.5 mm long.

BOTSWANA—N:—2124 (Toromoja): Toromoja (-BA), *Anderson 1* sub *Peterhouse 160* (K). N: Mumpswe Pan, 40 km. NNW. of mouth of Nata R., *Drummond & Seagrief 5172* (K) (specimen doubtful).

SW—2421 (Tsane): Tsane Pan (-BB), *Wild* 5126 (K).

S.W.A.—1813 (Ohopoho): Kaoko Otavi (-BC), *de Winter & Leistner* 5589 (K).

—1814 (Otjitundua): Dolomietpunt (-C), *Le Roux* 897 (PRE).

—1915 (Okaukuejo): Adamax (-BA), *Le Roux* 696 (PRE); E of Sprokieswoud, *Le Roux* 823 (PRE).

—1920 (Tsumkwe): Tsumkwe (-DA), *Giess, Watt & Snyman* 11104 (PRE).

—2016 (Otjiwarongo): Otjiwarongo, S of Sukses (-BC), *Tölken & Hardy* 965 (K, PRE).

—2116 (Okahandja): Okahandja (-DD), *Dinter* 145 sub SAM 70758, 146 sub SAM 70759 (SAM), 235 sub SAM 70762 (SAM).

—2215 (Trekopje): Neuschwaben near Karibib (-BB), *Seydel* 1068 (K).

—2216 (Otjimbingwe): Otjozondou (Otjosondou) (-AA), *Seydel* 3373 (L).

—2314 (Sandwich Harbour): Tsondab Vlei (-?), *Jensen* 2331 (PRE).

—2616 (Aus): Kuibis (-DB), *Range* 827 sub SAM 70675 (SAM).

Grid reference unknown: Salem, Tsoachabsand, 29 July 1898, *Dinter* 129 (Z, holotype).

TRANSVAAL—2725 (Bloemhof): Bloemhof, S.A. Lombard Nature Reserve (-DA), *Leistner* 47 (PRE).

Grid reference unknown: *Holub s.n.* (K).

O.F.S.—2926 (Bloemfontein): Bloemfontein (-AA), *Bolus s.n.* (BOL); Weed in Bloemfontein National Botanic Garden, *Brenan* 14093 (K, MO, NBG, PRE), 14094 (K).

CAPE—2520 (Mata Mata): Kalahari Gemsbok National Park, Kwang, Nosobrivier (-BA), *Barnard* 768 (PRE).

—2824 (Kimberley): 50 km. W of Douglas (-DB), *Compton* 23989 (NBG); Kimberley (-DD), *Moran s.n.*, p.p. (NBG).

—2921 (Kenhardt): Jagbult 64 km. W of Marydale (-DA), *Story* 1128 (PRE).

—2922 (Prieska): Prieska (-DA), *Bryant* 48 (K).

—3024 (De Aar): Rolfontein (-BB), *Jooste* 128 (PRE).

—3025 (Colesberg): about 14 km from Venterstad on Bethulie road (-DD), *Brenan* 14090 (K).

—3121 (Fraserburg): Fraserburg (-DC), *Bolus* 13435 (BOL).

—3125 (Steynsburg): Middelburg (-AC), *Theron* 83 (L, PRE); by Groote Vis R. on Spitskopvlei—Conway road NE of Graaff-Reinet (-CB), *Brenan* 14080 (K, NBG).

—3219 (Wuppertal): Cedarberg, Matjesrivier (-AC), *Wagener* 363, (NBG).

—3224 (Graaff-Reinet): Sunday's R. near Blue Gum House Farm (-DD), *Hilliard & Burt* 10701 (E); [Van] Ryneveld's Pass near Graaff-Reinet (-?), *Bolus* 360 (BOL).

—3321 (Ladysmith): Koup (-AB), *Compton 10399* (NBG).

Grid reference unknown: Grootfontein, *Rehmann s.n.* (K).

Without locality; *Krauss 777*, p.p. (K).

var. 'B'

Female perianth-segments in fruit 2.5–5 mm long.

S.W.A.—2218 (Gobabis): Gobabis, Farm Poortje (-BD), *Merxmüller & Giess 1147* (PRE).

—2317 (Rehoboth): N of Kalkrand on road to Rehoboth (-?), *de Winter 3509* (K, PRE).

—2718 (Grunau): Groot Karasberge, Wilmond (-BC), *Örtendahl (152) 459* (K, L).

CAPE—2723 (Kuruman): Albert (-BC), *Cooper 789* (K).

A. dinteri has been much misunderstood. In South Africa it has been confused with *A. thunbergii*, in spite of the careful distinctions drawn between the two species by Thellung in Ascherson and Graebner's *Synopsis der Mitteleuropäischen Flora* 5, 1 (1914). It has been equally misunderstood in Europe, mainly because it was not known as an adventive prior to 1914, and has only since then been recorded comparatively rarely in Germany and Sweden (Aellen in Hegi, *Illustrierte Flora von Mitteleuropa* ed. 2, 3, 2: 503 (1959). I have collected it once in Britain [v.c. 30, Bedfordshire, Flitwick Station, 1 Oct. 1949, *Brenan & Dony 9757* (Herb. Brenan)]. The majority of the numerous European records of *A. dinteri* refer to var. *uncinatus* Thell. which, for reasons given on p. 477 is here considered to be specifically separate from *A. dinteri*.

A. dinteri, even after the exclusion of var. *uncinatus*, is decidedly variable especially in the size of the perianth. It seems useful at present to recognise two subspecies and the varieties mentioned above. Their status is nevertheless uncertain and it really requires experimental cultivation to bring any certainty, though the variation would seem to be in large part genetically controlled.

Le Roux 696 and *823* and *Brenan 14093*, cited above under var. 'A', and *de Winter & Leistner 5574*, cited above under var. 'B', show very clearly that the leaves have on their upper side an irregular often lobed or even compound purplish blotch. This has been named f. *maculatus* Probst & Thell. [ex Probst, *Dritter Beitr. Adventiv-und Ruderalfl. von Solothurn und Umgebung*, reprinted from *Mitteil. Naturf. Gesellsch. Solothurn* 8: 59 (1928), nomen nudum; et ex Hegi, *Ill. Fl. Mitteleur.*, ed. 2, 3, 2: 503 (1950), germanice tantum descripta], forma nova. Folia supra macula purpurea in medio ornata. This was originally based on an adventive plant in Europe (I have been so far unable to locate the type material), and is analogous to *A. thunbergii* f. *maculatus* Thell. In Bloemfontein National Botanic Garden I collected a copious gathering of *A. dinteri*

with blotched leaves (*Brenan 14093*) among which were a few plants with leaves wholly green (*Brenan 14094*), otherwise identical. This variation thus is of trivial importance.

subsp. **brevipetiolatus** Brenan, subsp. nov.

Internodia etiam caulium praecipuum omnia brevia, usque ad 7 (–10) mm longa. Petioli omnes breves, usque ad 7 mm longi. Laminae parvae, usque ad 8 mm longae et 4 mm latae.

Type: South Africa, Bloemfontein, *Brenan 14095* (K, holotype; NBG, PRE, isotypes).

Internodes even on the main stems all short, up to 7 (–10) mm long. Petiole always short, up to 7 mm long. Leaf-lamina small, up to 8 mm long and 4 mm wide.

O.F.S.—2926 (Bloemfontein): Bloemfontein National Botanic Garden (–AA), *Brenan 14095* (K, holotype; NBG, PRE, isotypes).

CAPE—2824 (Kimberley): Kimberley (–DB), *Wilman s.n.* (K).

The material available of subsp. *brevipetiolatus* is still inadequate either to give a full conception of this taxon or to be certain of its status. The uniformly short petioles are very distinctive, however. *Brenan 14095* was collected at Bloemfontein growing with subsp. *dinteri* but distinct and without intermediates. Further knowledge may well show it to be a separate species. *Leistner 2976* (O.F.S., Willem Pretorius Game Reserve) may well be subsp. *brevipetiolatus*, but has somewhat larger foliage. More material of this taxon is much desired.

7. ***Amaranthus capensis*** Thell. in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 293 (1914); Adamson in JI S. Afr. Bot. 2, 4:193 (1936); Adamson in Adamson & Salter, Fl. Cape Penins. 361 (1950); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 502, fig. 232 (p. 472) (1959). Type: South Africa, *Ecklon & Zeyher 88* (lectotype, not seen).

A. blitum sensu Cooke & Wright in Thiselton-Dyer, Fl. Cap. 5, 1:411 (1910), pro parte quoad *Galpin 2015*, *Bowker s.n.*, non L.

Annual. Stems prostrate, radiating from rootstock, 50–250 (–600) mm long, ± branched especially in basal part, ± puberulous when young at least with very short straight or papilliform hairs, without crisped or elongate pubescence. *Leaves* with petiole 10–13 (–23) mm long, mostly short or very short; axils without spines; lamina obovate, 3–20 mm long, 2–10 (–15) mm wide, glabrous or subglabrous, ± attenuate at base, rounded and sometimes slightly emarginate at apex with mucro absent or very minute, green without purple blotches, with conspicuously undulate margins. *Inflorescence* of small dense axillary clusters

extending to near base of stem, often \pm confluent above; inflorescence thus leafy throughout. *Bracteoles* lanceolate to ovate-acuminate, shorter than perianth, with downwardly curved apex. ♂ *flowers* with $3 \pm$ ovate-elliptic shortly acuminate perianth-segments; *anthers* long-exserted, about 1–2 mm long. ♀ *flowers* with 3 unequal perianth-segments 2–5.5 mm long, variable in width (0.3–1 mm) \pm broadened and often curved outwards or hooked above with a close green reticulum of veins, obtuse or subacute sometimes acute at apex with a minute deflexed apiculus c. 0.10–0.25 mm long, usually 1–2 segments markedly broader and greener above than the third or all lanceolate and subulate-acuminate. *Stigmas* 0.5–1 mm long. *Fruit* obovoid to subglobose, shorter than perianth, circumscissile, smooth to somewhat rugose above. *Seed* glossy, brownish-black, about 0.75–1.5 mm in diameter; surface faintly reticulate and very finely roughened.

subsp. **capensis**

Female perianth-segments (in fruit) unequal, about 2–3.5 mm long, obovate or spatulate, with 1–2 markedly broadened and green above with a minute apiculus 0.1–0.25 mm long, often curved outwards but not subulate-uncinate.

TRANSVAAL—2531 (Komatipoort): Barberton (-CC), *Thorncroft* 882 (BM).

CAPE—3025 (Colesberg): about 14 km from Venterstad on Bethulie road (-DD), *Brenan* 14089 (BOL, G, K, M, MO, NBG, PRE, UPS).

—3026 (Aliwal North): Nieuwe Hantom (-CC), *Drège* sub SAM 19199 (SAM).

—3121 (Fraserburg): near Fraserburg (-DC), *Bolus* 13435 p.p. (BOL).

—3124 (Hanover): Hanover (-AB), *Sim* 6259 (PRE) (doubtful).

—3125 (Steynsburg): about 18.5 km N of Middelburg (-AC), *Acocks* 15695 (K, PRE).

—3224 (Graaff-Reinet): Graaff-Reinet (-BC), *Zeyher* 3 sub SAM 19198 (SAM); by Camdeboo R. about 30 km S of Graaff-Reinet by the Aberdeen road (-AC), *Brenan* 14074 (K).

—3318 (Cape Town): Middelburg. Grootfontein (-DC), *du Toit* s.n. (PRE).

—3383 (Willowmore): Willowmore (-AD), *Theron* 907 (K).

—3324 (Steytlerville): Steytleville (-AD), *Compton* 20309 (NBG).

—3418 (Simonstown): "Somerset" (?-BB), *Bowker* s.n. (K).

Grid references unknown: between Cape and Grahamstown, Ward 38 (E); Karieboomfontein, *Pearson* 3923 sub SAM 28373 (SAM).

subsp. **uncinatus** (Thell.) Brenan, comb. nov.

A. dinteri Schinz var. *uncinatus* Thell. in Scheuermann, 4/5 Jahresber. Niedersächs. B. V. Hannover, 1911/12: 74 (1913) (not seen); in Asch. &

Graebn., Syn. Mitteleur. Fl. 5, 1: 297 (1914); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 503, figure 233 (p. 473) (1959); Brenan in Watsonia 4, 6: 273 (1961). Type: numerous syntypes from Germany (adventive).

Female perianth-segments (in fruit) subequal, lanceolate, (2.5-) 4–5.5 mm long, gradually narrowed above to an elongate subulate point about 1–2.5 mm long, conspicuously hooked towards apex.

LESOTHO—2929 (Underberg): Sehlabathebe Reserve (-CC), Bayliss sub BRI 1316 (K).

CAPE—2723 (Kuruman): Albert District (-BC), Cooper 789 (BM, E, p.p., K).

—3027 (Lady Grey): Barkly East (-DC), Sim 20394 (PRE).

—3126 (Queenstown): Queenstown (-DD), Galpin 2015 (K, PRE) (see note below).

—3226 (Fort Beaufort): Swartkei ("Zwartkey") Shiloh, etc. (-BA), Baur 971 (K).

This species, indigenous to South Africa alone, has been neglected and poorly understood. Its neglect in South Africa has no doubt been due to the facts that it was first described in a flora of mid-Europe, and that it is still poorly represented in herbaria.

Thellung (*l.c.*, *supra*) cited three specimens with the original description: Ecklon & Zeyher 88 from South Africa, and three German specimens found as adventives (Rodleben near Rosslau, 1908, Zobel *s.n.*; Mannheim, 1909, Zimmermann *s.n.*; Döhrener Wollwäscherei near Hannover, 1911, Scheuermann *s.n.*). The first three were placed by Thellung under subvar. *microphyllus* (*l.c.* p. 294) and the Döhren plant under subvar. *elongatus* (*l.c.* p. 295). Neither of the subvarieties seems at present worth recognition, as habit and leaf-size are evidently too much affected by habitat conditions to be of taxonomic significance, and the size of the perianth-segments changes considerably between flower and fruit. These are the leading characters employed in distinguishing the subvarieties.

I have not seen type material of subvar. *elongatus* but I have had on loan from the Botanisches Museum der Universität Zürich the type of *microphyllus* (Germany, Hautwollfabrik Rodleben bei Rosslau (Anhalt), 1 Aug. 1908, Zobel *s.n.* (Z)), and it is typical *A. capensis*. I have no reason, however, in spite of having seen only one of the syntypes (I have not located the others), to doubt the interpretation of the species.

The taxonomy of *A. capensis* is not yet free from problems. Thellung [in Ascherson & Graebner, *Synopsis der Mitteleuropäischen Flora* 5, 1: 294 (1914)] suggested the possibility that it might be a slightly teratological form of *A. dinteri*. However, in 1976 I was fortunate enough to find *A. capensis* in some

abundance along a newly made roadside between Venterstad and Bethulie in Cape Province, South Africa (Brenan 14089), growing with *A. dinteri*, but very obviously quite distinct from that in habit, foliage and floral character, and without any sign of intermediates.

The subspecies *uncinatus*, hitherto considered as a variety of *A. dinteri*, has occurred on numerous occasions in Europe as an adventive, usually if not always introduced with wool [see Brenan in *Watsonia* 4: 273 (1961)]. The subspecies seems much more closely related to *A. capensis* than to *A. dinteri*. Although the extremes of typical *A. capensis* and subsp. *uncinatus* are clearly different, yet there are perplexing intermediates, and much variation in the upper part of the perianth-segments even on one and the same plant. The status of subsp. *uncinatus* requires further study, at present hampered by the lack of material from native habitats.

Galpin 2015 (Queenstown) is anomalous in resembling subsp. *uncinatus* but with very short female perianth-segments even in fruit (2–2.5 mm long). Further material is needed.

Thellung (*l.c.*) cited numerous European specimens (from Germany) with the original description of *uncinatus*. Although I have only so far seen a small piece of one of the originals, there is no reason to have any doubt about the interpretation of the taxon. Thellung subsequently named numerous other adventive specimens, including some from Britain, and the European material so far seen is rather uniform and very characteristic; and there is at Kew the above-mentioned fragment, sent by Thellung to Stapf, of one of the cited gatherings (Germany, Lauritz, Spremberg, 1890, *Riese s.n.*) which is exactly the taxon as usually interpreted.

8. *Amaranthus blitoides* S. Wats. in *Proc. Amer. Acad. Arts & Sci.* 12: 273 (1877); Thellung in *Asch. & Graebn., Syn. Mitteleur. Fl.* 5, 1: 290 (1914); Brenan & Sandwith in *Rep. Bot. Soc. & E. C.* 13: 269 (1948); Aellen in *Hegi, Ill. Fl. Mitteleur.*, ed. 2, 3, 2: 489, fig. 214 (p. 470) (1959). Type from North America.

Annual. Stems mostly prostrate, about 0.2–0.8 m long, usually much branched, when young subglabrous or very inconspicuously puberulous with very short papilliform or straightish hairs. *Leaves* with petiole 3–25 mm long, variable in length on a single plant; axils without spines; lamina oblanceolate to obovate, mostly 10–50 mm long, 3–17 mm wide, glabrous or subglabrous, cuneate-attenuate at base, obtuse to rounded and \pm mucronate at apex, without any purplish central blotch. *Inflorescence* of axillary dense to sometimes rather loose axillary clusters extending to near base of stem; clusters not or scarcely confluent above; inflorescence leafy throughout. *Bracteoles* of ♀ flower about as long as or rather shorter than the perianth. ♂ flowers with 4–5 ovate or ovate-elliptic perianth-segments with a short awn-like point about 0.25–0.6 mm long; *anthers*

exserted, about 0,8 mm long. ♀ flowers with (in fruit) 4–5 unequal oblong to ovate-oblong perianth-segments 2–3 mm long with greenish midrib not or scarcely branched above and not thickened above, mostly (at least the longer segments in each flower) acute at apex, with a very short point up to 0,2 mm long. *Stigmas* 0,25–1,0 mm long. *Fruit* ellipsoid, equalling or very slightly exceeding the longer perianth-segments, circumscissile, smooth to \pm rugose above. *Seed* subcircular to ellipsoid, glossy, blackish, 1,8–2 mm in diameter, with surface almost smooth or only very minutely roughened.

A. blitoides, native of North America, has been rather frequently recorded as an introduction in Europe. In South Africa the evidence of its occurrence is a single specimen collected in 1976.

CAPE—3318 (Bellville): Tygerberg Nature Reserve, Area E above dam (-DC), *Loubser 3485* (NBG).

The other species occurring in South Africa most likely to be confused with *A. blitoides* are *A. dinteri* and *A. thunbergii*. *A. blitoides* differs from both in having 4–5, not 3, perianth-segments and larger seeds. In addition *A. blitoides* differs from *A. dinteri* in the predominantly oblanceolate (rather than obovate) leaves; from *A. thunbergii* in the shorter indumentum on the young parts and in the much shorter points to the ♀ perianth-segments.

9. ***Amaranthus praetermissus* Brenan, sp. nov. (Fig. 2).**

A. angustifolius sensu Adamson in JI S. Afr. Bot. 2, 4: 194 (1936), saltem pro parte, non L.

A. schinzianus sensu Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr., 33 Amaranthaceae: 8 (1936) quoad spec. *Kinges 3464* et al. in nota citata, non Thell.

A. thunbergii sensu Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr., 33 Amaranthaceae: 8 (1936), pro parte, quoad *Marais 4499*, non Moq.

Ut videtur *A. schinziano* Thell. proxima sed segmentis perianthii florum fermineorum plerumque majoribus (saepius 1,5–3 mm nec 0,75–1,5 mm longis) apice in acumen conspicuum 0,25–1 mm. longum plerumque attenuatis fructus excedentibus. Auctoribus multis cum *A. graecizans* L. confusa, sed segmentis perianthii feminei 4–5 nec tantum 3 fructus superantibus facile distinguenda.

Annua, inermis. *Caules* primarii erecti, circiter 200 mm–1 m alti, praesertim basim versus crebre ramosi, glabri, laeves vel juventute praesertim perminute papilloso. *Folia* petiolo 1–15 (-30) mm longo; lamina oblanceolata, oblanceolato-oblonga vel paene linearis, plerumque 10–40 mm longa, 1–10 mm lata, glabra, basi in petiolum gradatim attenuata, apice obtusa vel subacuta et ibi mucrone 0,75–1,5 mm long praedita. *Inflorescentiae* fasciculis densis axillaribus fere usque ad caulis basim superne saepe confluentibus compositae, ubique hinc (nodis

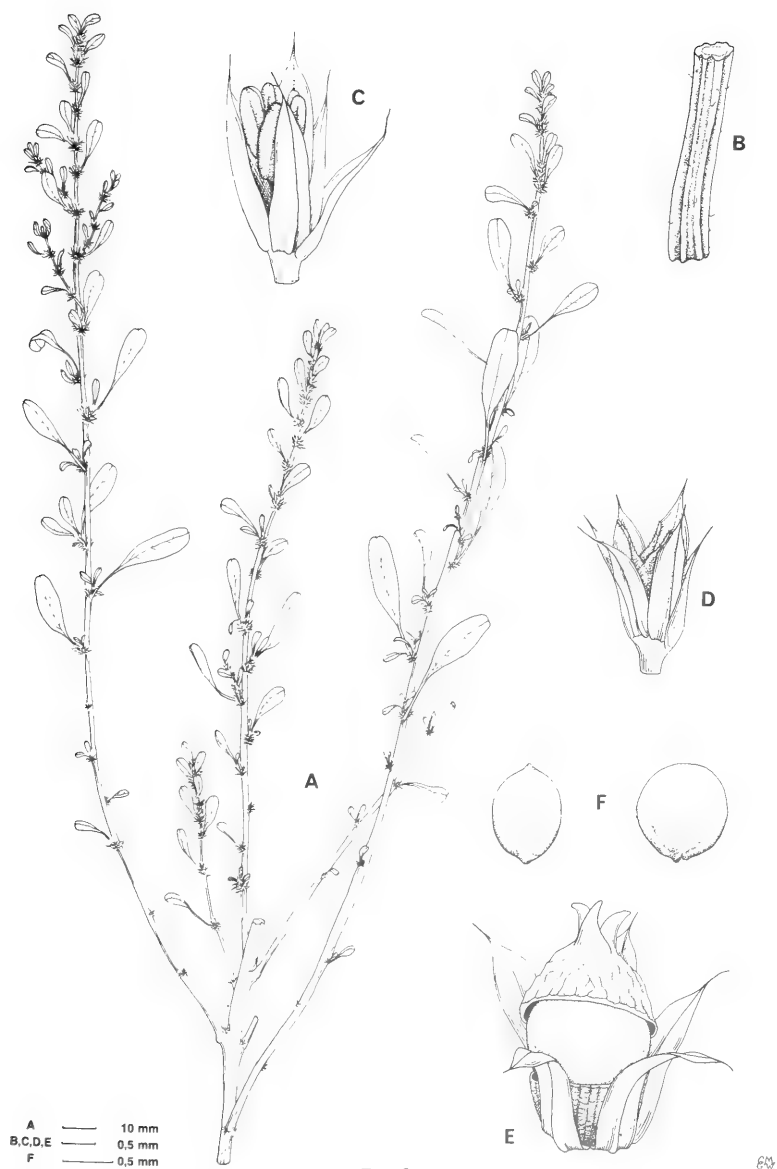


FIG. 2

Amaranthus praetermissus. A, habit. B, part of young stem to show indumentum. C, male flower. D, female flower. E, fruit dehiscent. F, seeds. From *Brenan 14143*.

paucis supremis raro exceptis) foliosae. *Bracteolae* lanceolatae, quam perianthium breviores, apice acuminatae. *Flores masculi* segmentis perianthii 4 ovatis circiter 2 mm longis apice mucrone erecto circiter 0,3 mm longo praeditis. *Antherae* circiter 0,75 mm longae, vix exsertae. *Flores feminei* segmentis perianthii 4-5 subaequalibus lanceolatis vel oblongo-lanceolatis vel nonnunquam oblanceolatis, superne costa viridi non vel leviter ramosa et in acumen erectum vel \pm patens 0,25-1 mm longum angustatis (vel nonnunquam plus minusve rotundatis). *Stigmata* 0,5-0,75 mm longa. *Fructus* ovoideus vel obovoideus, quam perianthium brevior, circumscissilis, superne conspicue rugoso-verrucosus. *Semina* nitida, fere nigra, elliptica vel rotundata, 1-1,2 mm longa, 0,75-1 mm lata, fere laevia.

Type: South Africa, Malalahoek 20 km N.E. of Messina, *Brenan 14143* (K, holotype; NBG, PRE, isotypes).

Annual. *Main stem* or stems erect, about 200 mm-1 m high, with numerous branches especially in lower part, glabrous, smooth or minutely papillose especially when young. *Leaves* with petiole variable in length, 10-15 (-30) mm long; axils without spines; lamina oblanceolate, oblanceolate-oblong or almost linear, mostly 10-40 mm long and 1-10 mm wide, glabrous, attenuate at base into the petiole, obtuse to subacute and distinctly mucronate (0,75-1,5 mm) at apex, green. *Inflorescence* of dense axillary clusters extending to near base of stem; clusters often confluent above; inflorescence thus normally leafy throughout (occasionally a very few of the topmost clusters appearing leafless). *Bracteoles* lanceolate, about half to three-quarters as long as perianth. *Male flowers* with 4 ovate perianth-segments about 2 mm long, with an erect mucro about 0,3 mm long at apex; *anthers* scarcely exserted, 0,75 mm long. *Female flowers* with 4-5 subequal perianth-segments 1,5-3 mm long, lanceolate to oblong-lanceolate or sometimes oblanceolate, at apex tapering (sometimes rounded) into an erect or somewhat spreading acumen 0,25-1 mm long; midrib green, not or somewhat branched above. *Stigmas* 0,5-0,75 mm long. *Fruit* ovoid or obovoid, shorter than perianth, circumscissile, coarsely rugose-warted above. *Seed* glossy, brownish-black, elliptic to almost round, 1-1,2 mm long, 0,75-1 mm wide, almost smooth.

ANGOLA—Mossamedes, 1859, *Welwitsch 6527* (K).

ZIMBABWE—E: Lower Sabi District: Rupisi Hot Springs, 28 Jan. 1948, *Wild 2308* sub Govt. Herb. 19061 (K).

—S: Sabi R., Birchenough Bridge, Jan. 1938, *Obermeyer 37472* (BOL); S: Gwanda District: Tuli Offices, 16 Feb. 1965, *Norris-Rogers 664* (K).

BOTSWANA—N:—1923 (Maun): Maun, above high flood level of Thamelakane R. (-CD), *Biegel & Russell 3723* (K, PRE).

- 2022 (Lake Ngami): N. of Ngwanalekau Hills (-DD), *Buerger 1151* (PRE).
—2026 (Nata): Moseitse R., 75 m from Francistown (-DA), *Richards 14607a* (K).
—2127 (Francistown): Francistown (-BA), *McClintock K37* (K); Tonota (-AD), *McClintock K38* (K); N: Tlalamabaie—Masu area, near Soa Pan, *Ngoni 314* (K).
SW:—2121 (Ghanzi): Ghanzi Camp (-DA), *Brown 7890* (K).
—2122 (Kobe): Kuke Pan (-AB), *van Son 28740* (BM, PRE).
—2324: Khutse (-AD), *Shaw 2* sub *Peterhouse 356* (K, PRE).
—2421 (Tsane): Tsane (Tsani) Police Station (-BB), *de Winter 7451* (K, PRE).
SE:—2422 (Mashi A Potsana): Mahudatlachi (Mahudutlake) Pan (-AB), *Cox 404* (K).
SE:—2426 (Mochudi): Mochudi. Phutodikobo Hill (-AC), *Naomi Michison 59, 60* (K).
S.W.A.—1719 (Runtu): Kapako Camp, 6 km W of Mupini Mission (-DC), *de Winter & Marais 4499* (PRE).
—1914 (Kamanjab): Kaross (-AD), *Thorne* sub *SAM 35712* (SAM).
—1918 (Grootfontein): Amkib near Grootfontein (-CA), *Schoenfelder 8452* (PRE).
—2114 (Uis): 24 km from Uis to Henties Bay (-BB), *Tölken & Hardy 826* (K, PRE).
—2115 (Karibib): Karibib (-DD), *Kinges 3464* (PRE).
—2116 (Okahandja): 110 km S of Otjiwarango on Okahandja road (-BB), *Hardy 2140* (K, PRE).
—2117 (Otjosondú): Quickborn (-AA), *Bradfield 210* (PRE).
—2214 (Swakopmund): Haigamkab (Haikamchab) (-DB), *Galpin & Pearson 7529* sub *SAM 1592* (K, PRE, SAM); 101 km E of Swakopmund (-?), *Hardy & de Winter 1397* (PRE).
—2217 (Windhoek): Windhoek (-CA), *Morgan 626/31* (BOL).
—? 2219 (Sandfontein): Farm Poortje (-?DA), *Merxmüller & Giess 1145* (PRE).
—2419 (Aranos): Farm Lekkerwater, 51 km E of Aranos (-AB), *van Vuuren & Giess 1104* (K, PRE).
—2718 (Grünau): 24 km N of Karasburg Drift, just S of Kanus railway siding (-DC), *Wilman 285* (BOL).
—2818 (Warmbad): Sandfontein (-DA), *Wilman* sub *SAM 28698* (SAM).
Grid references unknown: Omajume. *Volk 2939* (PRE); 40 km from Omitara, *Liebenberg 4585* (PRE).
TRANSVAAL—2229 (Waterpoort): Farm Rosenthal near Dongola (-BC), *Codd 4841* (K, PRE); Greefswaldt 89 km W of Messina (-AB), *Pienaar 282* (K,

PRE); Greefswaldt, *Theron 2774* (PRE); Langjan Nature Reserve (-CC), *Huntley 1803* (PRE), *Zwanziger 454* (PRE).

—2328 (Baltimore): Magaebas Nek Farm, Skrikfontein, 85 km NW of Potgietersrus (-?), *Maguire 1500* (NGB).

—2330 (Messina): Messina (-AC), *Moss & Rogers 95* (J), *Rogers 20040* (J); Malalahoek 20 km NE of Messina, *Brenan 14143* (K, holotype; NBG, PRE, isotypes); Tshipise (-CA), *Brenan 14172* (K, MO, PRE).

—2431 (Acornhoek): Satara, Kruger National Park (-BD), *van der Schijff 2268* (PRE).

—2527 (Rustenburg): Brits District, Farm Welgevonden (-?DB), *Mogg s.n.* (PRE).

Grid references unknown: Soutpansberg, Aerodrome koppie, *Verdoorn 2115* (PRE); Fourteen Streams, *Burt Davy 1587* (PRE).

CAPE—2723 (Kuruman): Batlharo (-AD), *Silk 193* (K).

—2824 (Kimberley): Kimberley (-DB), *Wilman 3292* (K), *Wilman s.n.* (K, PRE), *s.n.* (K), *s.n.* (BOL, PRE); 88 km W of Douglas, *Compton 23999* (NBG); Kimberley, Riet Pan, *Moran 15921* (BOL); Voet Pads Drift near Magersfontein (-DC), *Wilman s.n.* (PRE); Spytfontein, *Moss 15343* (BM); Gordonia District, Amob R., 80 km upwards from mouth (-?BA), *Lang 31750* (PRE).

—2922 (Prieska): Spitzkop, N of Nange R. (-?), *Bryant J48* (PRE).

—3025 (Colesberg): Oviston (-DA), *Jooste 547* (PRE).

—3224 (Graaff-Reinet): Graaff-Reinet (-BC), *Bolus 357* (BOL, K).

Grid references unknown: "in vinetis prope Wynberg", *Bolus 7051* (BOL); "Klip Drift, Herbert", *Moran 2* (K), *16641* (BOL).

Without locality: *Drège s.n.* (L).

A. praetermissus, although widespread and in places plentiful, has been consistently misunderstood. Usually it has been misnamed *A. angustifolius* Lam. or *A. graecizans* L. (the two names are synonymous and the latter the correct one). However, *A. graecizans* L., which is widespread in tropical Africa though apparently not reaching our area, is very easily separated by the ♀ flowers possessing only 3 perianth-segments not exceeding the fruit and normally lacking the acuminate apex so characteristic of our plant. In fact, *A. praetermissus* is apparently more closely related to *A. schinzianus* Thell. (though with a very different ♀ perianth) as was acutely noted by the late Dr A. W. Kloos on *Wilman 3292* at Kew (though most other specimens of this taxon were named by him *A. angustifolius* Lam., except for *Moran 2* which he correctly suggested as representing an undescribed species). Suessenguth & Podlech (*l.c.*, *supra*) also included *A. praetermissus* under *A. schinzianus* and cited several specimens in a note, recognising their difference from *A. schinzianus* and suggesting hybridisa-

tion between that an *A. thunbergii*. I am confident, however, that *A. praetermissus* is a distinct species and not a hybrid of such parentage.

A. praetermissus thus appears to be confined to the southern part of Africa from Angola, Botswana and Zimbabwe southwards. It should be looked for in Zambia.

10. ***Amaranthus schinzianus*** Thell. in Vierteljahrschr. Nat. Ges. Zürich **57**: 535 (1913); Adamson in JI S. Afr. Bot. **2**, 4: 195 (1936); Suessenguth & Podlech in Merxmüller, Prodr. Fl. Südwestafr., 33 Amaranthaceae: 8 (1966). Type: South-West Africa, "Gross Namaland", *Fleck 171 a* (Z, syntype; L, isosyntype).

A. blitum sensu Cooke & Wright in Thiselton-Dyer, Fl. Cap. **5**, 1: 411 (1910) pro parte, quoad Zeyher 1438, Bolus 11624, non L.

Annual. Stems prostrate to erect, 30–500 mm, \pm branched especially below, but sometimes throughout, glabrous. Leaves with petiole 10–15 mm long; axils without spines; lamina linear-oblongate to almost linear, 5–25 mm long, 0.5–5 mm wide, glabrous, gradually attenuate at base, obtuse and mucronate at apex. Inflorescence of small dense axillary clusters extending to or to near base of stems, clusters often confluent above; inflorescence leafy throughout. Bracteoles minute, ovate to lanceolate, shorter than perianth. σ flowers with 4 elliptic to oblong perianth-segments obtuse to subacute at apex; anthers about 0.5–0.7 mm long. ϕ flowers with (in fruit) (4–)5 subequal, spatulate or obovate perianth-segments 0.75–1.5(–1.75) mm long, whitish except for green midrib which is unbranched or nearly so above, rounded or obtuse (and sometimes very shortly mucronate) at apex. Stigmas 0.25–0.4 mm long. Fruit obovoid-turbinate, exceeding perianth, ? indehiscent or circumscissile, coarsely warted in upper part, brownish when ripe. Seed ellipsoid-rounded or round, glossy, blackish, 1 mm in diameter, almost smooth.

A. schinzianus is confined to South and South-West Africa.

S.W.A.—2316 (Nauchas): between Dubaigabis and Gründoorn (Groendorn) (-DD), Pearson 3173 sub SAM 28372 (SAM); Klein Karas, Groendorn, Örtendahl 367 (K, PRE).

—2317 (Rehoboth): Rehoboth Farm Duineveld REH 437 (-DC), Giess, Volk & Bleissner 6779 (PRE).

—2516 (Helmeringhausen): road from Farm Landsberg to Helmeringhausen (-DD), Kinges 2157 (PRE); dry bed of Helene R., Farm Helmeringhausen, Kinges 2190 (PRE).

—2616 (Aus): Luederitz, ravine S. of Aus, Farm Klein Aus (-CA), Kinges 2324 (PRE).

—2618 (Keetmanshoop): Paradies (-AC), Range 1311 sub SAM 70764 (SAM); Keetmanshoop (-CA), Lubenberg 5199 (PRE).

—2718 (Grünau): Groot Karasberge, Witmond (-BC), Örtendahl 461 (BOL).

K, PRE); Klein Karas (-CA), *Dinter* 4949 (PRE), *Örtendahl* 178 (K, PRE); 8 km on Great Karasberg road from Karasburg-Grünau road (-DC), *Oliver & Steenkamp* 6264 (K).

—2818 (Warmbad): S. of Warmbad (-BD), *Pearson* 4025 (BOL); near Orange R. at Goodhouse (-CC), *Wilman* 259 (BOL).

—2819 (Ariamsvlei): Nakop railway station (-BB), *Marais* 1112 (K, PRE); 3 km W. of Nakop (Nakob), *Theron* 1951 (K, NBG, PRE); 36 km W. of Ariamsvlei along Karasburg-Upington road (-?BB), *Davidse & Loxton* 6420 (PRE).

Grid reference unknown: "Gross-Namaland" Apr. 1889, *Fleck* 171a (Z, syn-type; L, isosyn-type).

CAPE—2921 (Kenhardt): De Hoek, W.S.W. of Kenhardt (-AC), *Leistner* 2356 (K, PRE).

—3118 (Vanrhynsdorp): Bitterfontein (Bosjesmanslop) (-AB), *Zeyher* 1438 (BOL, K, NBG, PRE, SAM).

—3120 (Williston): Rietkolk (-AB), *Acocks* 9615 (PRE).

—3221 (Merweville): Prince Albert Road (-DC), *Pillans* 16467 (BOL).

—3321 (Ladysmith): Koup (-AB), *Rehmann* 2983 (Z, holotype), *Esterhuysen* 4510 (BOL).

—3322 (Oudtshoorn): Boter Kraal near Prince Albert (-AA), *Bolus* 11624 (BOL, K).

—3223 (Rietbron): Nelspoort (-AA), *Lewis* 4243 sub SAM 67517 (SAM).

This is a very distinct species on account of its leafy inflorescence entirely axillary combined with 4–5 spatulate to obovate ♀ perianth-segments shorter than fruit. The very narrow foliage is also characteristic. The fruits are conspicuously strongly warted and although apparently sometimes circumscissile, seem to dehisce very tardily, often remaining closed until brown and apparently ripe. I suspect that they may sometimes fall off the plant without dehiscing.

Through the courtesy of the Director of the Botanische Garten und Institut für systematische Botanik der Universität Zürich, I have received on loan the type of *Amaranthus schinzianus* (*Rehmann* 2983), which agrees well with the species as it has been generally interpreted. *Fleck* 171a, also received on loan, is annotated by Thellung "*Amarantus schinzianus* Thellung sp. nov. f. *monstrosa*", but seems to be only a stage of *A. schinzianus* with the fruits enlarged and ripe.

It may be of interest to put on record here that *A. schinzianus* Thell. has occurred as an adventive in Britain [S.W. Yorkshire, v.-c. 63: Corporation Tip, Heckmondwike, 8 Oct. 1964, *J. E. Lousley & C. E. Shaw* W2408 (K!)]. No doubt it was introduced with wool waste. Its occurrence was unknown to me when I revised *Amaranthus* in Britain [*Watsonia* 4: 261–280 (1961)].

11. *Amaranthus deflexus* L., Mant. Pl. Altera 295 (1771); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 313 (1914); Burt Davy. Fl. Transv. 181

(1926); Adamson in *Jl S. Afr. Bot.* 2, 4: 194 (1936); Adamson in Adamson & Salter, *Fl. Cape Penins.*: 361 (1950); Aellen in *Hegi, Ill. Fl. Mitteleur.*, ed. 2, 3, 2: 504, fig. 235 (p. 473) (1959); Brenan in *Watsonia* 4, 6: 274 (1961); Henderson & Anderson, *Common Weeds S. Afr.* 106, fig. 52 (1966); Suessenguth & Podlech in *Merxmueller, Prodr. Pl. Südwestafr.*, 33 *Amaranthaceae*: 8 (1966); Ross, *Fl. Natal* 158 (1972). Type: cultivated at Uppsala, Herb. Linnaeus 1117/18 (LINN, holotype).

A. viridis sensu Cooke & Wright in *Thiselton-Dyer, Fl. Cap.* 5, 1: 411 (1910), non L.

Perennial. *Stems* annual, prostrate or ascending, \pm numerous from root-stock, usually with short, sometimes longer, lateral branches about 0.1–0.9 m long, glabrous or glabrescent below, \pm pubescent with crisped hairs when young. *Leaves* with petiole usually 5–30 mm long; axils without spines; lamina ovate to lanceolate or almost elliptic, often rhombic, 5–60 mm long, 4–30 mm wide, glabrous or nearly so above, shortly and inconspicuously pubescent especially on margins and midrib and lateral nerves beneath, \pm cuneate or cuneate-subtruncate towards base, the base itself \pm attenuate, subacute to obtuse and sometimes slightly emarginate at apex, green and without darker blotches. *Inflorescence* terminal, spiciform or compactly pyramidal-paniculate, 20–120 mm long and about 5–20 mm wide; shorter spikes or clusters often also present in upper and middle axils. *Bracteoles* about half as long as perianth-segments or less. σ^7 *flowers* fewer than and mixed with f , mostly towards ends of spikes or branches, with 2–3 elliptic-acuminate unequal perianth-segments 0.75–1.5 mm long. f *flowers* with 2–3 linear to oblong-oblancoate, acute or very shortly acuminate perianth-segments about 1.5–2 mm long, hyaline with a green midrib excurrent in a very short mucro about 0.1 mm long. *Stigmas* 0.25–0.4 mm long. *Fruit* clearly exceeding the perianth, indehiscent, smooth or nearly so, 1.75–3 mm long, rounded or obtuse at apex. *Seeds* very glossy, ellipsoid-compressed, blackish-brown, 1–1.2 mm long, 0.75–0.8 mm wide, smooth or almost so, scarcely reticulate.

Widely spread in the tropics and subtropics and common in southern Europe. Native home uncertain but probably temperate South America.

S.W.A.—2217 (Windhoek): Windhoek (-CA), *Seydel* 4070 (K).

— ? 2717 (Windhoek): station ? Leutwein (?-CC), *Dinter* 4258 (BM, SAM).

TRANSVAAL—2528 (Pretoria): Pretoria, near station (-CA), *Sandwith* 185 (K, PRE); Pretoria, Corellilaan, Les Marais, *Hanekom* 1352 (K, PRE).

— 2628 (Johannesburg): near Wattles (-AC), *Moss* 8572 (BM); weed, University of the Witwatersrand (-AA), *Moss* 22683 (J).

O.F.S.—2829 (Harrismith): Rensburgskop, Swinburne (-AD), *Jacobz* 551 (K).

—2926 (Bloemfontein): Bloemfontein, Park Road (-AA), *Potts Blf. U. 7924* (K, PRE).

NATAL—2830 (Dundee): Dundee (-AA), *Truscott 23* (PRE).

—2930 (Pietermaritzburg): Pietermaritzburg, Alexandra Park (-CB), *Huntley 243* (PRE).

LESOTHO—2927 (Maseru): Maseru (-AD), *Williamson 316* (K); Roma (-BC), *Schmitz 284* (PRE).

CAPE—2824 (Kimberley): Kimberley, street (-DB), *Wilman* sub SAM 25348 (SAM).

—3125 (Steynsburg): Middelburg (-AC), *Acocks 15676* (K, PRE).

—3318 (Cape Town): Cape Town (-CD), *Moss 4350* (BM, J); Sea Point (-CD), *Treleven 214* sub SAM 1149 (SAM), sub *Dummer 1274* (E); Kirstenbosch (-CD), *Compton 19423* (BOL, NBG); Cape Town, Rosebank, near station, *Sandwith 186* (K); Rondebosch, *Adamson 2842* (BOL); Stellenbosch (-DD), *Duthie 386* (BOL); Onderpapegaaiberg, *Taylor 5650* (K, PRE).

—3319 (Worcester): Karoo Garden, Worcester, weed (-CB), *Brenan 14047* (K).

—3326 (Grahamstown): Grahamstown (-BC), *MacOwan 3419* (K, SAM).

—3418 (Simonstown): Cape Flats (-BA), *Rehmann 2009* (BM); Somerset West (-BB), *Parker 3793* (BOL, K, NBG).

A. deflexus is one of the most easily recognised species. It is unusual in having a distinctly perennial rootstock from which annual stems arise in a more or less clustered or radiating way. Among the species with terminal inflorescences the large smooth almost inflated fruits, rounded or obtuse at apex and much exceeding the narrow perianth-segments, are most distinctive. The 2–3 perianth-segments and short bracteoles are also shared only with *A. viridis* among the species with terminal inflorescences, but the fruits are totally different. The ellipsoid outline of the seeds is also unusual.

12. *Amaranthus lividus* L., Sp. Pl. 990 (1753); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 313 (1914); Adamson in Jl S. Afr. Bot. 2, 4: 194 (1936); Adamson in Adamson & Salter, Fl. Cape Penins. 361 (1950); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 505, fig. 236 (p. 473) (1959). Type: 18th century cultivated material (BM, neotype); see Townsend, Fl. W. Pakistan, 71 Amaranthaceae: 17 (1974).

Variable in habit, annual or sometimes a short-lived perennial. *Stems* prostrate to erect, 40–750 mm long or tall, numerous and radiating from base or simple and erect, \pm branched, glabrous. *Leaves* with petiole 20–100 mm long, often with considerable range of variation on one plant; axils without spines; lamina ovate to ovate-elliptic, 4–120 mm long, 4–100 mm wide, glabrous, broadly cuneate or rounded-cuneate towards base, shortly attenuate at base it-

self, at apex normally conspicuously emarginate, but sometimes almost rounded. *Inflorescence* lateral and terminal, the terminal part usually leafless, spiciform or paniculate, sometimes leafy to near apex. ♂ *flowers* towards end of spikes or inflorescence branches, with 3 elliptic concavo-convex perianth-segments about 0.5–1.5 mm long, obtuse or subacute at apex. ♀ *flowers* with 3 (sometimes 4–5 in the cultivated forms of subsp. *lividus*, not found yet but perhaps to be expected in the area) perianth-segments, linear-oblong to oblong-subspathulate, 0.75–2 mm long, acute to obtuse at apex, but not or only minutely mucronate or acuminate, with green central part near apex. *Stigmas* 0.25–0.5 mm long. *Fruit* longer than perianth, 1.5–2.5 mm long, indehiscent, compressed, rotund to shortly pyriform. *Seed* glossy, 1–1.5 mm in diameter, blackish-brown, very faintly and minutely roughened, faintly reticulate.

subsp. ***polygonoides*** (Moq.) Probst, Wolladventivfl. Mitteleur. 74 (1949); Brennan in *Watsonia* 4, 6: 275 (1961). Types from Java and Brazil.

Euxolus viridus (L.) Moq. var. *polygonoides* Moq. in DC., Prodr. 13 (2): 274 (1849).

Female perianth-segments usually obtuse, about 1 mm long. Fruit about 1.5 mm long. Seed 0.8–1 mm in diameter.

CAPE—3318 (Cape Town): Newlands (-CD), *Brenan 14100* (BOL, K, NBG).

—3418 (Simonstown): Princess Vlei (-AB), *Walgate 683* (BOL, PRE); Zeekoevlei (Zeikoei Vlei) (-BA-BB), *Walgate* (BOL).

NATAL—2930 (Pietermaritzburg): Pietermaritzburg (-CB), *Garrett 15* (E); Durban District, Merebank Central (-DD), *Bajinath 2930* (PRE).

A. lividus is widespread in the tropics and warmer regions of the world, and subsp. *polygonoides* in the tropics of both hemispheres. Further synonymy of subsp. *polygonoides* will be found in Brennan (1961), *supra*.

A. lividus is generally easily recognisable. The normally conspicuously emarginate leaves are characteristic. The plant is quite glabrous and the inflorescences usually in part terminal and leafless. The compressed fruits are indehiscent and distinctly longer than the perianth. This combination of characters makes *A. lividus* generally unmistakable, although it is very variable in other ways. In South Africa it is only a rare weed.

Recently Fillias, Gaulliez & Guédès, in *Taxon* 29, 1: 149–50 (1980), have advocated the resurrection of the name *Amaranthus blitum* L. to replace *A. lividus* L. Because of persistent past confusion with *A. graecizans* L. (starting with Linnaeus himself!), such a revival serves no good purpose. The rejection of *A. blitum* L. as a *nomen confusum* has been therefore formally proposed by Brennan & Townsend in *Taxon* 29, 5–6: 695–6 (1980).

13. *Amaranthus viridis* L., Sp. Pl. ed. 2, 1405 (1763); Burt Davy, Fl. Transv. 181 (1926); Brenan in Watsonia 4, 6: 275 (1961); Henderson & Anderson, Common Weeds S. Afr. 106 (1966). Type: Herb. Linnaeus 1117/15 (LINN, lectotype).

A. gracilis Desf., Tabl. Ecole Bot. 43 (1804); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 335 (1914); Adamson in Jl S. Afr. Bot. 2, 4: 195 (1936); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 503, fig. 234 (p. 473) (1959); Ross, Fl. Natal 158 (1972).

Short-lived perennial. *Main stems* erect or decumbent, up to 1 m long, simple or several from near base, themselves with \pm numerous branches, with some short crisped inconspicuous pubescence near young apices, soon glabrous or subglabrous. *Leaves* with petiole variable in length, the longer ones 20–60 (–100) mm long; axils without spines; lamina mostly ovate, sometimes ovate-elliptic, often somewhat rhombic, mostly 20–70 (–80) mm long, 15–50 (–68) mm wide, glabrous or with some very short inconspicuous pubescence on midrib and lateral nerves especially beneath, broadly cuneate or cuneate-rounded towards base, with base itself abruptly attenuate, obtuse or sometimes rounded at apex and usually slightly emarginate and shortly mucronate, green and without darker blotches. *Inflorescence* a green, \pm branched terminal panicle with leafless spiciform branches 20–120 mm long, often interrupted below, often also with branches from upper axils. *Bracteoles* shorter than the flowers. σ^7 flowers few, intermixed with f in inflorescence, but especially towards end of branches, with 3 broadly elliptic concave perianth-segments. f flowers with 3 narrowly oblong to oblong-spathulate perianth-segments about 1–1.5 mm long, whitish with green midrib which is often thickened above, mucronate or not at apex. *Stigmas* 0.25–0.4 mm long. *Fruit* subequalling or slightly exceeding the perianth, indehiscent or irregularly splitting, not circumscissile, very strongly rugose all over. *Seed* only slightly shining, blackish, 1–1.25 mm in diameter; surface minutely and very closely reticulate with the areoles of the reticulum marked by slightly raised verrucae.

Found throughout the tropics and subtropics of the world. Its native home is doubtful; Thellung (1914) discusses the problem, suggesting tropical Asia as the most likely area.

TRANSVAAL—2528 (Pretoria): Pretoria, Corellilaan, Les Marais (–CA), *Hanekom* 1347 (K, PRE).

NATAL—2930 (Pietermaritzburg): Isipingo Beach (–DD), *Ward* 5253 (K), *Ward* 6298 (K).

—2931 (Stanger): Durban, Burman Bush (–CC), *Bourquin* 216 (E); Durban Bayhead (–DD), *Ward* 5115 (K, PRE); Durban, Natal Herbarium grounds, *Schweickerdt* 1364 sub NH 30580 (K, PRE).

CAPE—2824 (Kimberley): Kimberley (–DB), *Wilman* 5708 (K, NBG, PRE).

Among the species with terminal panicles or spikes, *A. viridis* is very easily distinguished by the indehiscent fruits closely and regularly wrinkled and not or only slightly exceeding the perianth. From all except *A. lividus* and *A. deflexus* the flowers with only 3 perianth-segments are quite distinctive. The sculpturing of the seed-surface is also anomalous, although requiring the use of a compound microscope for it to be seen clearly. However, the seeds have a much less glossy testa than its relatives, and this alone can clinch the identity. The seeds, however, must be removed from the green pericarp before examination.

The life-form of *A. viridis* has been misunderstood. Thellung (*l.c.*, *supra*) says that it is annual, querying whether it may be perennial. Aellen (*l.c.*, *supra*) describes it as annual without comment. Examination of various herbarium specimens at Kew led me to doubt very much whether it was always annual. During a visit to Las Palmas, Canary Islands, in spring 1978, I saw numerous plants of *A. viridis* and paid special attention to their life-form. *All* gave evidence of being short-lived perennials with annual stems radiating from the top of a vertical taproot going to about 200–300 mm deep in the soil. It seems, however, possible that flowering may take place in the first year after germination.

14. *Amaranthus muricatus* (Moq.) Hieron. in Bol. Acad. Cienc. Córdoba 4: 421 (1881); Thellung in Asch. & Graebn., Syn. Mitteleur. Fl. 5, 1: 339 (1914); Burt Davy, Fl. Transv. 181 (1926); Adamson in Adamson & Salter, Fl. Cape Penins.: 360 (1950); Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 491, figure 216 (p. 470) (1959); Henderson & Anderson, Common Weeds S. Afr. 106 (1966). Type from Argentina.

Euxolus muricatus Moq. in DC., Prodr. 13, 2: 276 (1849).

Perennial. Stems apparently annual, prostrate or ascending, \pm numerous from a stout rootstock, usually with numerous branches, 0.15–0.4 m long, glabrous or sometimes slightly and inconspicuously pubescent near inflorescence. *Leaves* with petiole 5–10 (–15) mm long; axils without spines; lamina linear to linear-lanceolate, rarely lanceolate, 15–80 mm long, 2–10 mm wide, glabrous or almost so, attenuate towards base, usually obtuse and often slightly emarginate or in very narrow leaves acute at apex, green and without darker blotches. *Inflorescence* terminal, narrow, spiciform, leafless, interrupted or continuous, often branched especially below, 30–120 mm long, 5–8 mm wide. *Bracteoles* about half to two-thirds as long as perianth-segments. σ^7 flowers fewer than and mixed with f , with 5 elliptic-subacute perianth-segments about 1–1.5 mm long. f flowers with normally 5 (occasionally 4) narrow, oblanceolate, obtuse to subacute perianth-segments about 1.5–2 mm long, hyaline with a green not or very shortly excurrent midrib. *Stigmas* 0.15–0.25 mm long. *Fruit* subequalling to very shortly exceeding the perianth, indehiscent, closely and clearly rugose-muricate all over, 1.75–2 mm long, with a short beak-like projecting apex. *Seeds* with only moderate glossiness, blackish-brown, 1–1.25 mm long, 0.8–1 mm wide;

surface minutely and very closely reticulate with the areoles of the reticulum marked by slightly raised verrucae.

Native of temperate South America (Argentina, Paraguay, Uruguay). Introduced and locally established in southern Europe, North America and South Africa. A rare adventive in northern Europe.

TRANVAAL—2528 (Pretoria): Pretoria, Eastern Street (-CA), *Burt Davy s.n.* (PRE).

—2628 (Johannesburg): 15,2 km S.E. of Johannesburg (-AC), *Mogg 34191* (PRE).

O.F.S.—2926 (Bloemfontein): Bloemfontein, Eagle's Nest (-AA), *Potts 2579* (K, L), *Mostert 647* (PRE).

CAPE—2824 (Kimberley): Kimberley (-DA), *Acocks 8572* (PRE).

—3318 (Cape Town): Green Point Common (-CD), *Salter 8382* (BOL).

—3324 (Graaff-Reinet): By Camdeboo R., about 30 km S. of Graaff-Reinet by Aberdeen road (-AC), *Brenan 14073* (K).

A. muricatus is immediately recognised among the South African species of *Amaranthus* with terminal inflorescences by its very narrow leaves and perennial habit. The closely muricate fruits and (under the compound microscope) closely reticulate-verrucose seeds, however, indicate a possible relationship with *A. viridis*, which has much broader leaves and only 3 perianth-segments to the flower.

Although the basionym of *A. muricatus* is often attributed to "Gillies ex Moq.", this is incorrect. Moquin (*l.c.*) published the species as *Euxolus muricatus*, citing "*Amaranthus muricatus* Gillies ! in herb. Hook." as a synonym. There is no indication that Gillies was in any way responsible for *Euxolus muricatus*.

I am much indebted to Dr. T. Myndel Pedersen, of the University of Copenhagen, for help over the nomenclature of this species and for indicating Hieronymus as the originator of the combination *Amaranthus muricatus*.

15. *Amaranthus standleyanus* Parodi ex Covas in *Darwiniana* 5: 339 (1941); *Brenan in Watsonia* 4, 6: 278 (1961). Type from Argentina.

A. vulgatissimus sensu Thellung in *Asch. & Graebn., Syn. Mitteleur. Fl.* 5, 1: 343 (1914); *Aellen in Hegi, Ill. Fl. Mitteleur., ed. 2, 3, 2: 493, figure 219* (p. 471) (1959); et auct. al. eur., non *Spegazz.*

Annual. Stems erect to decumbent, 0,2–0,7 m high, \pm branched, shortly and inconspicuously crisped-pubescent when young, often glabrescent later. *Leaves* with petiole very variable in length, often short (10 mm or less) but usually some on main stems long (20–70 mm); axils without spines; lamina ovate to elliptic, often subrhombic, about 10–50 mm long, 5–30 mm wide, glabrous or nearly so above, shortly and inconspicuously pubescent especially on margins and midrib

and lateral nerves beneath, broadly cuneate to cuneate-attenuate towards base, obtuse to rounded at apex, sometimes subacute, often emarginate and minutely mucronate, green and without darker blotches. *Inflorescence* of dense sessile clusters, all axillary or the upper condensed into a leafless spiciform panicle up to 50 mm long. *Bracteoles* much shorter than the perianth-segments. ♂ *flowers* fewer than ♀, mostly towards ends of spikes or clusters, with 5 elliptic, acute, scarcely acuminate perianth-segments about 1.5 mm long. ♀ *flowers* with 5 strongly obovate-spathulate perianth-segments about 2–3 mm long, the upper part broad, about 0.75–1 mm wide, spreading, whitish with a green midrib and rounded with a short often patent mucro at apex, below abruptly tapering into a narrow claw about 0.2 mm wide. *Stigmas* about 0.4–0.5 mm long. *Fruit* about as long as or slightly shorter than perianth, indehiscent, the lower part containing the seed strongly and closely rugose all over; the upper part narrower and smooth. *Seed* glossy, deep chestnut-brown, about 0.8–1.1 mm in diameter, almost smooth, not or scarcely reticulate.

A native of Argentina, rarely introduced elsewhere, e.g. South Africa and Europe.

S.W.A.—2216 (Otjimbingwe): Otjozondú (Otjosondú) (-AA), *Seydel* 3373 (L).

CAPE—2922 (Prieska): Prieska (-DA), *Bryant* 890 (K), 47a (K).

A. standleyanus is very easily distinguished by the combination of 5 very strongly spathulate perianth-segments on the ♀ flowers, indehiscent fruits strongly and closely wrinkled in the lower part and smooth in the upper.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the help received from numerous people during the course of this study. Particular thanks are due to my colleague Mr. C. C. Townsend of the Royal Botanic Gardens, Kew, who has himself made important contributions to our knowledge of *Amaranthus* but who has generously made his experience and advice freely available throughout.

I am also most grateful to Professor Brian Rycroft, Director of the National Botanic Gardens, Kirstenbosch, South Africa, and to Dr. John Rourke, Curator of the Compton Herbarium, for permission to work in that Herbarium and to examine *Amaranthus* there. An equal debt of gratitude is due to Dr. Bernard de Winter, Director of the Botanical Research Institute, Pretoria, for similar facilities there. Grateful thanks are also due to Professor E.A.C.L.E. Schelpe for facilities kindly given at the Bolus Herbarium, Cape Town. All these herbaria have also been kind enough to make subsequent loans.

To the authorities of the following other herbaria, whose material I have examined, I am also grateful:

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Leiden, Rijksherbarium;

London, British Museum (Natural History).

BIOLOGICAL NITROGEN FIXATION IN A NORTHERN TRANSVAAL SAVANNA

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ABSTRACT

The rate at which whole soil samples reduce acetylene was determined in a savanna at Nylsvley, Northern Transvaal. Activity was found from early January to mid-April. Peak activity occurred late in February. From the results it was calculated that the annual rate of nitrogen fixation probably lies between 29 and 86 kg N ha⁻¹ depending on whether, in this system, the reduction of 9 or 3 moles of acetylene are equivalent to the fixation of one mole of dinitrogen.

Nodulated legumes appear to be responsible for most if not all of the nitrogen fixation. All the legumes in the area except *Burkea africana* were found to be nodulated and capable of nitrogen fixation.

Evidence was obtained that during the acetylene reduction trials, the soil samples initially absorbed a small amount of ethylene. Although autoclaving the soil samples largely abolished the absorption, the process is considered to be a physical characteristic of the soil rather than a microbial one since it ceases after a few hours in unsterilized soil.

UITTREKSEL

BIOLOGIESE STIKSTOFBINDING IN NOORD-TRANSVAAL SAVANNA

Die tempo waarteen ongefraksioneerde grondmonsters asetileen reduseer, is in 'n savanne te Nylsvley, Noord-Transvaal bepaal. Aktiwiteit is van vroeg in Januarie tot middel April waargeneem met piekwaardes laat in Februarie. Uit die resultate blyk dit dat die jaarlikse tempo van stikstofbinding waarskynlik tussen 29 en 86 kg N ha⁻¹ is afhangende daarvan of die reduksie van 9 of 3 mol asetileen in die sisteem ekwivalent is aan die binding van een mol stikstofgas.

Genoduleerde peulplante is skynbaar vir meeste, of selfs alle stikstofbinding verantwoordelik. Daar is vasgestel dat alle peulplantsoorte in die gebied, met die uitsondering van *Burkea africana*, wortelknoppies besit en in staat is om asetileen te reduseer.

Daar is gedurende die asetileenreduksiebepalings aanduidings gevind dat die grondmonsters aanvanklik klein hoeveelhede etileen absorbeer. Alhoewel outoklaving grootliks verhoed het dat die grondmonsters daarna etileen opneem, word die etileenopname tog as 'n fisiese kenmerk van die grond eerder as 'n mikrobiologiese verskynsel gesien aangesien dit in ongestertiliseerde grond na 'n paar uur ophou.

INTRODUCTION

After Dilworth (1966) discovered that nitrogenase is capable of reducing acetylene to ethylene, Hardy *et al.* (1968) were quick to recommend that this attribute of nitrogenase be used to measure the rate of biological nitrogen fixation in the laboratory and the field. Since then Steyn and Delwiche (1970), Copley and Reuss (1972) and Vlassak *et al.* (1973) have employed the techni-

que in attempts to determine the annual rate of dinitrogen fixation in native grasslands.

The Council for Scientific and Industrial Research of South Africa is currently co-ordinating the Nylsvley Savanna Ecosystem Project (Huntley, 1978). One aspect of the project requires that an estimate be made of the rate at which nitrogen is annually being fixed in the ecosystem. This paper is a publication of the Savanna Ecosystem Project and reports on results that were obtained during 1974 to 1976 by means of the acetylene reduction method.

MATERIAL AND METHODS

Main experiment

The study was undertaken on a portion of the Nylsvley Provincial Nature Reserve in the Northern Transvaal (latitude S 24° 29', longitude E 28° 42'). The study area occurs on a plateau 1 100 m above sea level with sandy latosols and a climate that is typical of most areas occupied by savanna in the Republic of South Africa. It has a hot, wet season lasting from November through March, during which period 79 % of the mean annual precipitation of 630 mm is received (Huntley, 1978). From late April to the end of August, the climate is cool and dry while September and October are generally hot and dry.

The study area lies within Veld Type 18 of Acocks (1975) which is referred to as "Mixed Bushveld". The vegetation is an open savanna with *Burkea africana* the dominant tree species and *Eragrostis pallens* the dominant grass. Several legume species which are known to be capable of producing root nodules (Grobelaar *et al*, 1967; Grobbelaar and Clarke, 1972, 1974, 1975) occur scattered in the grass layer in low densities.

After many preliminary studies during 1974 and 1975 the following survey procedure was finally decided on: a straight line, 399 m long was marked out in the study area by means of 400 iron pegs spaced 1 m apart. This line served as a reference line for a hypothetical rectangular grid 399 m long and 29 m wide with lines 1 m apart running parallel to the boundaries of the grid and intersecting one another at 12 000 points. Each point of intersection on the grid was a potential soil sampling point. The grid was subdivided longitudinally into 40 subsections 10 m × 29 m in size and containing 300 potential soil sampling points each. One sampling point (which had not been sampled previously) in each subsection of the grid was sampled on each sampling date, thus yielding 40 sampling points selected at random per sampling date.

For each sampling date, the sampling points on the grid were selected by means of a table of random numbers (Snedecor, 1953). In the final experiment, the grid was sampled on the following 13 occasions: 1975/10/28, 1975/11/18, 1975/12/09, 1976/01/06, 1976/01/27, 1976/02/24, 1976/03/23, 1976/04/14, 1976/05/25, 1976/06/29, 1976/08/03, 1976/09/09 and 1976/09/30.

Two cylindrical soil cores with a cross-sectional area of 25 cm^2 were collected about 5 cm apart at each sampling point by means of a hammer-driven stainless steel soil borer. The soil samples were taken to a depth of 40 cm (1 dm^3 of soil) unless rock occurred at a shallower depth. Each soil sample was immediately hermetically sealed in a wide-mouthed glass container with a total capacity of about $1\ 100\text{ cm}^3$. The screw caps of the flasks were each fitted with a rubber serum bottle stopper.

Of the two soil samples from one sampling point, one was used as a control by not enriching it with acetylene. Approximately one tenth of the air in the other flask was replaced by commercial acetylene from a cylinder by means of the apparatus that is diagrammatically depicted in Figure 1, as follows: some of the air in flask A was withdrawn through the syringe needle B, by opening stopcock J until the pressure in the flask had dropped by the required amount as indicated by the mercury manometer C. (In practice H was mounted on the roof of a Volkswagen minibus while A, C, D and E were set up inside the rear luggage compartment of the minibus and F and G stood on the ground.) After it had been established that the flask did not leak, acetylene which had been scrubbed in concentrated H_2SO_4 to remove acetone vapours, was allowed to enter flask A through stopcock K until the gas pressure inside the flask became equal to atmospheric pressure.

The flask was disconnected from the syringe needle and shaken for a few seconds in order to facilitate the mixing of the acetylene, air and soil in the flask. A 2 cm^3 sample of the gas phase was now withdrawn from the control flask as well as from the acetylene-enriched flask by means of a gas syringe. The gas samples were introduced into 2 cm^3 glass serum bottles by the displacement of water (see Figure 2A) and sealed under water by means of a rubber serum bottle stopper.

The flasks were incubated in the shade at ambient temperature for 4 h. After the first 1.5 h, a 2 cm^3 sample of the gas phase was taken from each flask and stored as described above. At the end of the incubation period, i.e. after a further 2.5 h, a third 2 cm^3 sample of the gas phase of each flask was taken.

The gas samples were analysed in the laboratory for their ethylene concentration by means of gas-liquid chromatography, using a 1 cm^3 gas sample for each analysis. The gas samples were withdrawn from the serum bottles by displacement with water (Figure 2B). For the GLC, a 3 m Porapak R column with an internal diameter of 1.5 mm was used at 60°C in conjunction with a flame ionisation detector.

The volume of gas that was enclosed in the flask with the soil was calculated from the difference between the total volume of the flask and the volume of the soil sample. The latter was determined by displacing water in a measuring cylinder.

In calculating the rate of nitrogen fixation, it was assumed that for every 3 to

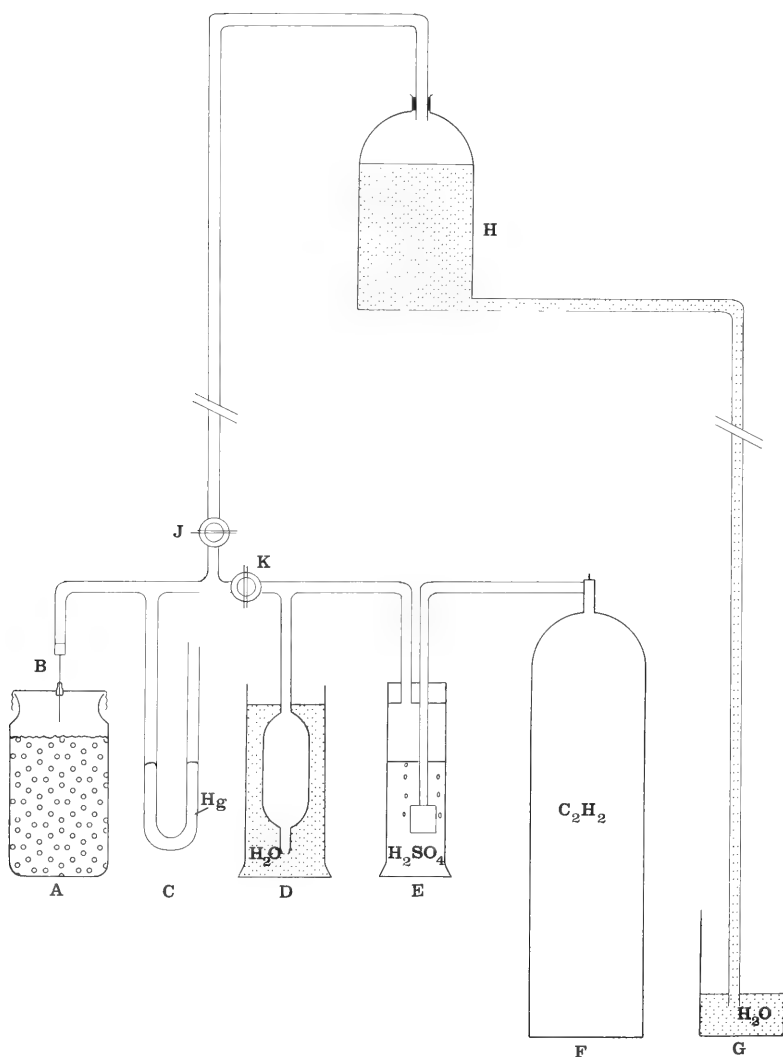


FIG. 1.

Diagrammatic representation of apparatus used in the field for replacing about one tenth of the air enclosed within a soil sample, by acetylene.

A = soil sample in flask fitted with a rubber serum stopper in its screw cap; B = syringe needle; C = mercury manometer; D = escape for excess acetylene through water; E = scrubber with conc. sulphuric acid; F = cylinder compressed acetylene; G = bucket for collecting water draining from H which is mounted about 2 m above G; J and K = stopcocks.

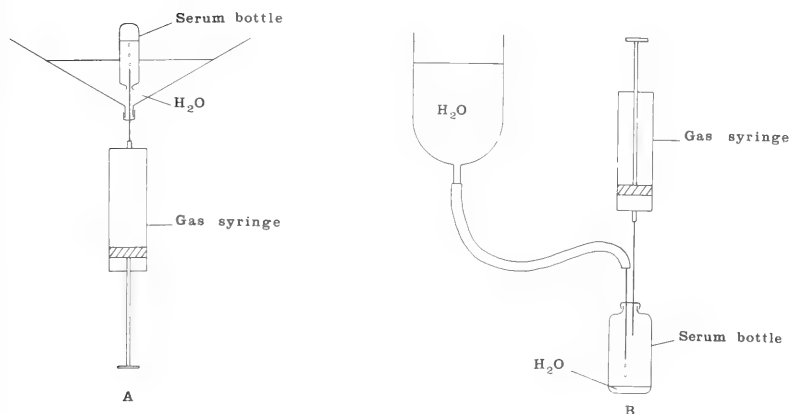


FIG. 2.

(A) Apparatus for injecting gas sample into serum bottle for storage.

(B) Withdrawal of gas sample from storage serum bottle for GC analysis.

9 moles of ethylene produced, one mole of dinitrogen would have been fixed as is claimed by Steyn and Delwiche (1970). It was also assumed that under the conditions under which the experiment was carried out, one mole of ethylene occupied 28.6 dm³.

Supplementary experiments

From preliminary experiments it became obvious that in many cases the soil samples yielded a negative rate of ethylene production—a phenomenon that could be observed due to the fact that the commercial acetylene that was used invariably contained some ethylene as an impurity. As a consequence the initial ethylene concentration varied between 4 and 18 n moles per cm³ incubation gas mixture. Changes in the rate of ethylene absorption with time were investigated. The effect of mixing the soil and acetylene containing air by briefly shaking the flask was also studied.

In another experiment, ten soil samples which absorbed ethylene were flushed with air late on the same day that the soil samples were collected in the field, by evacuating them three times by means of a water pump and allowing acetylene-free air to enter the flasks. The rubber serum bottle stoppers in the lids of the flasks were replaced by cotton wool plugs and five of the flasks were autoclaved for 1 h at 240 kPa after which all ten of the flasks were left overnight in the laboratory at room temperature. The following day, all of the flasks were re-incubated with acetylene in the usual way except that the ethylene concentration of the incubation gas mixture was increased to 300 n moles per cm³ gas mixture.

TABLE 1.

List of plant species occurring in the Nylsvley study area whose unwashed roots, shoots and soil were separately tested for acetylene reducing activity during February 1975.*

MONOCOTYLEDONES**POACEAE**

- Elionurus argenteus* Nees
- Schizachyrium sanguineum* (Retz.) Alst.
- Andropogon schirensis* Hochst.
- Cymbopogon marginatus* (Steud.) Stapf ex Burtt Davy
- Hyperthelia dissoluta* (Nees ex Steud.) Clayton
- Trachypogon spicatus* (L.f.) Kuntze
- Diheteropogon amplexans* (Nees) Clayton
- Digitaria eriantha* Steud.
- Cenchrus ciliaris* L.
- Aristida argentea* Schweick.
- A. congesta* Roem. et Schult. subsp. *congesta*
- Pennisetum patens* Gand.
- Eragrostis pallens* Hack.

COMMELINACEAE

- Commelina africana* L.

LILIACEAE

- Asparagus suaveolens* Burch.

VELLOZIACEAE

- Xerophyta retinervis* Bak.

DICOTYLEDONES**AIZOACEAE**

- Gisekia pharnaceoides* L.

ROSACEAE

- Parinari capensis* Harv.

MIMOSACEAE

- Elephantorrhiza obliqua* Burtt Davy

CAESALPINIACEAE

- Burkea africana* Hook.
- Cassia mimosoides* L.

FABACEAE

- Indigofera oxytropis* Benth.
- I. sordida* Benth.
- Tephrosia longipes* Meissn. var. *lurida* (Sond.) Gillet
- T. lupinifolia* (Burch.) DC.
- T. semiglabra* Sond.
- Rhynchosia monophylla* Schltr.

DICHAPETALACEAE

- Dichapetalum cymosum* Engl. et Prantl

TILIACEAE

- Grewia flavescens* Juss.

STERCULIACEAE

Waltheria indica L.

OCHNACEAE

Ochna pulchra Hook.

COMBRETACEAE

Terminalia sericea Burch. ex DC.

CONVOLVULACEAE

Ipomoea obscura (L.) Ker-Gawl. var. *fragilis* (Choisy) A. Meeuse

ACANTHACEAE

Crabbea hirsuta Harv.*Justicia minima* A. Meeuse

RUBIACEAE

Oldenlandia herbacea (L.) Roxb.*Pygmaeothamnus zeyheri* (Sond.) Robyns

* Species are arranged alphabetically within genera. The genera are arranged according to the system of de Dalla Torre and Harms (1963).

During preliminary trials, the roots of several of the common plant species were dug out and shaken free of most of the adhering sandy soil. A sample of the soil was also rapidly sieved free of roots. Samples of the shoots, roots and sieved soil were separately incubated in 300 cm³ flasks with and without acetylene as described above and tested for acetylene reduction.

RESULTS

The control soil cores without the acetylene enrichment did not release any ethylene and therefore any ethylene production was solely the result of acetylene reduction.

During the preliminary studies, it was established that all the legume species in the study area except *Burkea africana* usually have *Rhizobium*-type root nodules during the growing season and that these nodulated roots reduce acetylene at a relatively high rate (0–0.7 μ moles acetylene reduced per hour by a gram of fresh roots depending on the number and condition of the root nodules). The roots of none of the non-legume species tested (see Table 1) produced clear evidence of acetylene reducing activity. In no case did the shoots or sieved soil reduce acetylene.

Although the rate and duration of ethylene absorption varied considerably from one soil sample to the next, the results depicted in Figure 3 are typical of the majority of cases which did not show any acetylene reducing activity. By shaking the flask immediately after introducing the acetylene, the absorption of ethylene can be restricted almost wholly to the first 1.5 h of the incubation period during which time the nitrogen-fixing activity of nodulated roots in the soil should not have declined significantly in most cases.

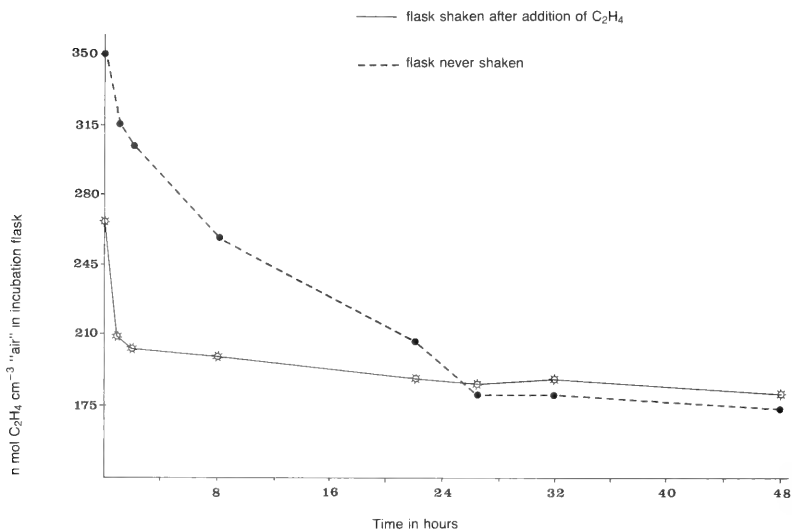


FIG. 3.

Decrease in ethylene conc. of incubation gas mixture while testing soil sample for acetylene reducing activity. In the one case (—), the flask was shaken gently for a few seconds after the ethylene was added but before the first ethylene determination was carried out. In the other case (---), the flask was never shaken. Both incubation flasks initially contained the same ethylene concentration.

From the results in Table 2, it is clear that the absorptive capacity of a soil sample can be largely restored by aerating the soil after an initial exposure to ethylene. Autoclaving the soil severely reduces the ability of the soil to absorb ethylene.

The results of the main experiment are summarised in Table 3 and the results in Table 3 which deals with the second part of the incubation periods are graphically represented in Figure 4. The acetylene reducing activity is limited mainly to the months January to April and appears to reach a peak late in February.

From Table 4 it is clear that despite an initial 1.5 h incubation period 209 of the 520 soil samples continued to show a net absorption of ethylene, albeit small amounts, during the second stage of the incubation period. Only 58 of the 520 soil samples yielded ethylene production rates in excess of 0.35 μ mole per hour during the second stage of the incubation period.

TABLE 2.

Effect of ventilating and autoclaving ethylene-absorbing Nylsvley soil samples on subsequent absorption rates

Soil Sample	Rate of ethylene absorption (n mol. h ⁻¹ per soil sample*) during			
	Initial incubation		Subsequent incubation after soil ventilated	
	1st part of incub. period (1,5 h)	2nd part of incub. period (2,5 h)	1st part of incub. period (1,5 h)	2nd part of incub. period (2,5 h)
	Soil not autoclaved		Soil not autoclaved	
1	1 713	49	734	119
2	804	10	664	182
3	804	7	839	91
4	734	24	699	101
5	629	7	874	66
Mean:	937	19	762	112
	Soil not autoclaved		Soil autoclaved	
6	1 783	45	280	-164
7	1 748	- 7	245	- 10
8	1 189	-10	315	-133
9	1 049	10	-559	133
10	734	66	245	- 17
Mean:	1 301	21	105	-38

* Cylindrical soil sample with 25 cm² cross sectional area 40 cm long.

Sampling sites that yielded strong positive results initially could not be correlated with the presence of any particular plant species or other feature. In fact, at only 4 of the 58 sampling points referred to above, was a nodulating legume species recorded within a metre of the sampling point.

On one occasion those soil samples that yielded strongly positive results were carefully searched for legume root nodules. In seven of the ten cases legume-like root nodules were found despite the fact that legumes were not observed within a metre of the sampling points. A day after the initial soil samples were taken, three soil samples were collected from the immediate vicinity of 6 "active sites" and 6 "inactive sites". Some of the new soil samples were active and others inactive, irrespective of whether they were taken in the vicinity of a sampling point which initially provided an active or an inactive soil core.

On several occasions active soil samples were re-incubated 24 h after they were initially collected. In all cases it was found that the acetylene reducing activity had completely disappeared. In other cases "active" soil samples were continuously incubated for 24 hours and tested periodically for acetylene reduc-

TABLE 3.

The rate of acetylene reduction by Nylsvley soil samples during different times of the year.

Sampling Date	Rate of acetylene reduction (n mol. h ⁻¹ per soil sample)*	
	First part of Incubation period (1,5 h)	Second part of incubation period (2,5 h)
1975-10-28	-1 643	0
1975-11-18	- 629	- 35
1975-12-09	- 105	0
1976-01-06	175	385
1976-01-27	594	594
1976-02-24	-35	1 469
1976-03-23	-3 357	350
1976-04-14	-1 678	839
1976-05-25	-1 923	0
1976-06-29	-2 133	35
1976-08-03	-2 063	105
1976-09-09	- 524	- 70
1976-09-30	-1 049	-210

* Each figure is the mean of 40 determinations. Cylindrical soil samples with a cross sectional area of 25 cm² and a length of 40 cm were used.

ing activity. The activity invariably decreased with time and disappeared completely within 24 h.

If the soil underneath 25 cm² surface area reduces acetylene at a constant rate of 1,5 μ moles h⁻¹, and if the reduction of 3 moles of acetylene is equivalent to the reduction of one mole of dinitrogen, this rate of acetylene reduction would amount to an annual rate of dinitrogen fixation of 490 kg ha⁻¹. In Figure 4, the area beneath the curve represents 0,176 of the area underneath the line for a constant rate of acetylene reduction of 1,5 μ mole h⁻¹ per soil sample.

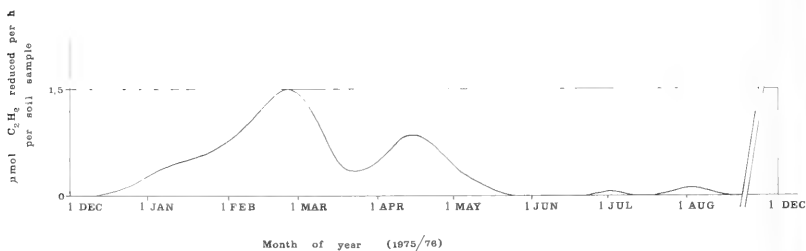


FIG. 4.

Changes in the mean acetylene reducing activity (mean of 40 determinations) of soil samples taken from Nylsvley at different times of the year. Each cylindrical soil sample had a cross sectional area of 25 cm² and a length of 40 cm.

Table 4. Frequency distribution of acetylene reduction values obtained for soil samples at Nylsvley.

Sampling date	Number of soil samples that yielded acetylene reduction values ($\mu\text{ mol. h}^{-1}$ per soil sample) between											
	-10,6 to -14,0	-7,1 to -10,5	-3,6 to -7,0	-0,36 to -3,5	-0,01 to -0,35	0,00 to 0,35	0,36 to 3,5	3,6 to 7,0	7,1 to 10,5	10,6 to 14,0	14,1 to 17,5	17,6 to 21,00
First part of incubation period (1,5 h)												
1975-10-28	0		1	30	8	1		0		0	0	0
1975-11-18	0		1	28	7	4		0		0	0	0
1975-12-09	0		0	1	31	8		0		0	0	0
1976-01-06	0		0	4	28	4		2		0	0	0
1976-01-27	0			3	12	15		8		0	0	0
1976-02-24	0		4	20	3	3		5		3	1	0
1976-03-23	1	5	10	14	8	1		1		0	0	0
1976-04-14	0		11	20	4	2		0		0	0	1
1976-05-25	0		3	35	1	1		0		0	0	0
1976-06-29	0		2	38	0	0		0		0	0	0
1976-08-03	0		4	34	2	0		0		0	0	0
1976-09-09	0		0	27	10	3		0		0	0	0
1976-09-30	0		0	33	6	1		0		0	0	0
Total	1	5	36	287	120	43	18	4	4	1	0	1
Second part of incubation period (2,5 h)												
1975-10-28	0	0	0	0	4	36	0	0	0	0	0	0
1975-11-18	0	0	0	0	29	11	0	0	0	0	0	0
1975-12-09	0	0	0	0	20	20	0	0	0	0	0	0
1976-01-06	0	0	0	0	15	19	5	1	0	0	0	0
1976-01-27	0	0	0	0	13	17	8	2	0	0	0	0
1976-02-24	0	0	0	1	6	15	13	3	1	0	0	0
1976-03-23	0	0	0	0	11	21	7	1	0	0	0	0
1976-04-14	0	0	0	1	10	18	10	0	0	0	0	1
1976-05-25	0	0	0	2	21	14	3	0	0	0	0	0
1976-06-29	0	0	0	0	16	22	2	0	0	0	0	0
1976-08-03	0	0	0	0	5	35	0	0	0	0	0	0
1976-09-09	0	0	0	1	23	16	0	0	0	0	0	0
1976-09-30	0	0	0	9	22	9	0	0	0	0	0	0
Total	0	0	0	14	195	253	48	7	1	1	0	1

* Cylindrical soil sample with a 25 cm² cross sectional area and a length of 40 cm.

From this, it would appear that the annual rate of dinitrogen fixation for the study site on Nylsvley is equal to about $(0,176 \times 490) = 86$ kg N per hectare. If, on the other hand as many as 9 moles of acetylene are reduced for one mole of dinitrogen fixed, the annual rate of nitrogen fixation at the Nylsvley study site approximates 29 kg N per hectare.

DISCUSSION AND CONCLUSIONS

Because the rate of ethylene absorption by soil samples declined rapidly with time, the process appears to be a physical rather than a microbial attribute of the soil despite the fact that autoclaving the soil largely abolished this characteristic.

Because of the low frequency of "active" soil samples, and the inability to predict which soil cores would yield positive results in the acetylene reduction assay, it was impractical to attempt to experimentally determine the equivalence between an acetylene reduction rate and the rate of dinitrogen fixation for the system under consideration. The widest recorded limits for such equivalence values appears to be 3 and 9 (Steyn and Delwiche, 1970). Even when an equivalence value of 9 is used, a rate of dinitrogen fixation is obtained for Nylsvley which is much higher than the annual rate of 0,4–3 kg N per hectare which other workers (Steyn and Delwiche, 1970; Copley and Reuss, 1972; Vlassak *et al.*, 1973) have recorded by means of the acetylene reduction method for North American temperate grasslands.

The relatively harsh and aerobic treatment to which the soil samples were subjected in the present study probably precluded the detection of nitrogen fixation by the type of system which Dobereiner (1973) claims to be important in tropical grasslands. Since all the available evidence points to nodulated legumes as the major, if not exclusive, dinitrogen fixing agents at the study site, the acetylene reduction method used was adapted to register its activity. In Dobereiner's work it is essential that soil cores be disturbed as little as possible or that they are pre-incubated for many hours under low oxygen tensions before the acetylene reduction assay is performed on them. Under the latter conditions the acetylene reducing activity of nodule bearing detached legume roots will be wholly lost. As it is, the present results are based on an incubation period which started 1,5 h after the soil sample was taken and in the case of some of the relatively active soil samples it was apparent that the activity started to decline during the second stage of the incubation period.

The observed presence in most of the active soil samples of legume root nodules directly supports the contention that these organs are important nitrogen fixing agents in the study site. The presence of root nodules at long distances from legume shoots is in agreement with the fact that the root systems of many of the plants in this area spread laterally for a considerable distance. In fact, it was observed that several legume species, such as *Elephantorrhiza obli-*

qua and *Cassia mimosoides* produce long rhizomes which interconnect widely spaced shoots. The decline of the acetylene reducing rate of active soil samples to virtually nil in the course of 24 h is also in agreement with the contention that legume root nodules rather than free-living nitrogen fixing bacteria are responsible for most, if not all the observed activity.

During the test period, the overall oxygen concentration in the incubation flasks could have decreased very slightly whilst the overall carbon dioxide concentration could have increased by as much as five fold (Bezuidenhout, J. J.: Department of Microbiology and Plant Pathology, University of Pretoria, pers. comm.). Although such changes should be detrimental to the activity of legume root nodules, it should stimulate the activity of certain free living nitrogen fixing bacteria and the type of system which Dobereiner (1973) has recently studied intensively. In the present case, however, the acetylene reducing activity of all the active soil samples that were incubated continuously for 24 h declined to virtually nil. It must therefore be assumed that the rates of acetylene reduction that were observed were probably wholly due to nodulated legume roots and represent an underestimation of the real rates. On the other hand, it must be borne in mind that the soil samples were generally collected late in the morning. If the acetylene reducing activity of the plants in question has a pronounced diurnal rhythm with peak activity late in the morning (as has been recorded for soybeans by Sloger *et al.* (1975)), the observed rates of acetylene reduction should be decreased by about half when it is used as the mean rate for the diurnal cycle.

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POLYPLOIDY, CHROMOSOME INTERCHANGE AND LEAF SURFACE ANATOMY AS INDICATORS OF RELATIONSHIPS WITHIN *HAWORTHIA* SECTION *COARCTATAE* BAKER (LILIACEAE—ALOINEAE)

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ABSTRACT

Original observations of the leaf surfaces and the number and morphology of the chromosomes were made on 282 plants of *Haworthia* section *Coarctatae* Baker from 26 localities in the Grahamstown/Port Alfred area of Cape Province, South Africa. Diploids ($2n = 14$), and all levels of polyploidy up to hexaploid were found in the area; also 14 chromosome interchanges and a small number of deletions and inversions were detected.

S.E.M. studies revealed that stomatal types can be characterised for *Haworthia coarctata* Haw. and *H. reinwardtii* Haw. sensu lato. Epidermal sculpturing is more frequently typical of individual populations, although some taxa were shown to be exceptionally variable within a population. A positive relationship was found between cell surface area and ploidy level.

The distribution of the interchanges gave no indication of inter-population relationships, but the observations on ploidy levels combined with those on anatomical features revealed that there are several relict diploid populations, from one of which polyploids have arisen to produce typical (i.e. tetraploid) *H. coarctata*. This has increased further in ploidy level to produce hexaploids of the same species and of *H. glauca* (S.D.) Bak.

Haworthia reinwardtii is normally diploid, but indications have been found of an eastward progression towards polyploids in the Chalumna area.

UITTREKSEL

POLIPLOÏEDIE, CHROMOSOOMWISSELING EN BLAAROPPERVLAKTE-ANATOMIE AS AANWYSERS VAN VERWANTSKAPPE IN *HAWORTHIA* SEKSIE *COARCTATAE* BAKER (LILIACEAE—ALOINEAE)

Oorspronklike waarnemings van die blaaroppervlaktes en die getal en morfologie van die chromosome is op 282 plante van *Haworthia* seksie *Coarctatae* Baker van 26 lokaliteite in die Grahamstad-Port Alfred-streek van die Kaapprovinsie, Suid-Afrika, gemaak. Diploëde ($2n = 14$) en alle vlakke van poliploëdie tot en met hexaploëdie is in die streek gevind; ook 14 chromosoomwisselings en 'n klein getal segmentverliese en omkerings is ontdek.

A.E.M.-studies het aan die lig gebring dat stomatipes vir *Haworthia coarctata* Haw. en *H. reinwardtii* Haw. sensu lato gekarakteriseer kan word. Opperhuidgraving is meer dikwels tipies van individuele bevolkings, al is sommige taksa as uiters veranderlik binne 'n bevolking bewys. 'n Positiewe verwantskap is gevind tussen seloppervlaksarea en poliploëdievlak.

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Die verspreiding van die omkerings het geen aanwysing van tussenbevolkingsverwantskappe gegee nie, maar die waarnemings van ploëdie-vlakke saamgevat met die van anatomiese kenmerke het aangedui dat daar verskeie diploëdie oorblyfselbevolkings is, en van een hiervan het poliploëdie tot stand gekom en tipiese (d.w.s. tetraploëdie) *H. coarctata* geproduseer. Die ploëdie hiervan het verder toegeneem en hexaploëdie van hierdie soort en van *H. glauca* (S.D.) Bak. geproduseer.

Haworthia reinwardtii is gewoonlik diploëdie, maar aanduidings is gevind van 'n ooswaartse reeks na poliploëdie in die Chalumna-streek.

INTRODUCTION

Little previous work has been reported on the anatomy of the leaf epidermis of *Haworthia* species. Cutler (1978a) showed that in *H. reinwardtii* f. *chalumensis* differences in ploidy level and some chromosome interchanges could be detected by observation of the cuticular sculpturing, the shape of the outer cell walls and details of stomatal structure. He has also indicated the probable taxonomic significance of cuticular sculpturing in other *Haworthia* species (Cutler, 1979), and there is now extensive evidence that sculpturing and stomatal structure are under rigid genetical control and can be used as very precise guides to the identity of taxa within the *Aloineae* (Brandham and Cutler, 1978; Cutler and Brandham, 1977).

It has already been shown that *H. reinwardtii* f. *chalumensis* is extremely unstable with regard to its chromosome complement, in which interchange hybridity is widespread (Brandham, 1974). This high frequency is unique in the *Aloineae*, more interchanges having been found in f. *chalumensis* than in the rest of the *Aloineae* put together. We therefore decided to look to the west of the area where f. *chalumensis* grows and investigate other populations of the group to which the taxon belongs (the section *Coarctatae* Baker of *Haworthia*) with the object of determining: a) the frequency and distribution of chromosome interchanges and other structural chromosome mutations, and b) whether any which were found had an effect on the morphology of the leaf surface.

Bayer (1976) has reviewed the taxonomy of *Haworthia*, and his findings with respect to *H. reinwardtii*, *H. coarctata*, their many varieties and forms and related species are particularly interesting. In his attempts to rationalise a complex problem he suggested a geographical and morphological basis for the recognition of *H. reinwardtii* and *H. coarctata* (Bayer, 1973).

Initial observations on stomatal details of plants collected by ourselves and/or Bayer from the Eastern Cape Province, indicated on the map (Fig. 1), showed some puzzling discontinuities when considered with Bayer's revised names for the many forms of *H. reinwardtii* and *H. coarctata* described from that area. A combined cytological and anatomical approach seemed appropriate to try to interpret the significance of these anomalies and to see whether a greater understanding of the complex interrelationships of the plants concerned could be achieved.

In addition, a marked variation in epidermal cell and stomatal size was found to exist between plants from different localities, and an investigation was carried out to determine whether this variation was correlated with differences of ploidy level.

MATERIAL AND METHODS

Material

Living material was collected from 282 plants growing in 26 localities in the general area of Grahamstown, Cape Province by Bayer or by Bayer, Brandham and Cutler (Table 1, Fig. 1). Plants of *Haworthia* sect. *Coarctatae* form extensive clumps of prostrate branches rooting along their length, and it was necessary to collect only the tip of one branch from each for cultivation and subsequent anatomical and cytological study. Thus unnecessary damage to the populations of these uncommon succulents was avoided. Plants were cultivated at Kew and representative vouchers are deposited in the Kew Herbarium (K).

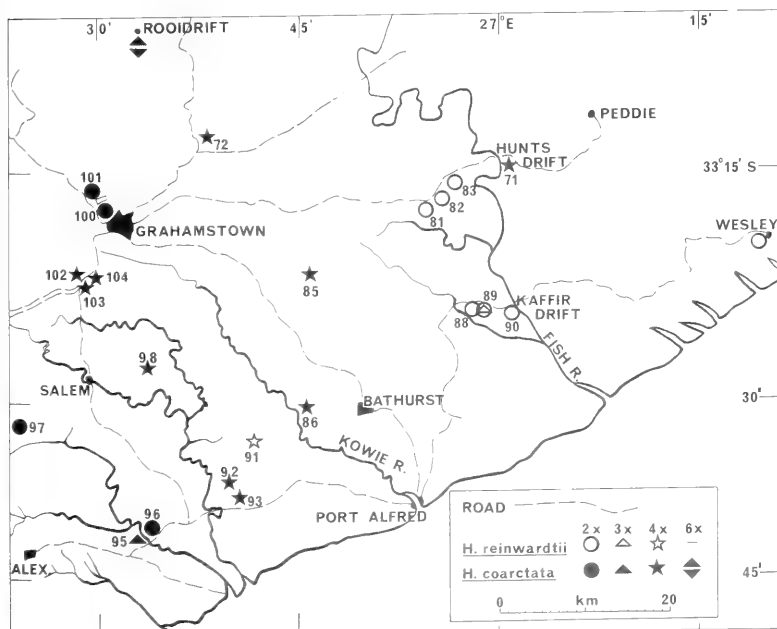


FIG. 1.

Map of the Grahamstown-Port Alfred area showing the location of the majority of the sampled sites of *H. coarctata* and *H. reinwardtii* (see Table 1), also the ploidy level of the plants at each site.

TABLE 1.
Origin of material, chromosome number and distribution of chromosome mutations.

Species	Loc. no.	Locality	2n	No. of plants studied	Chr. aberration and frequency	Fig.
<i>Haworthia coarctata</i> Haw.	71	Hunt's Drift	28	11	None	—
<i>H. coarctata</i> subsp. <i>adelaidensis</i> (von Poelln.) Bayer	72	Queens Road, Ecce Pass 13 km N E Grahamstown	28	11	2 with INT. 1 4 with INT. 2	4a 3f, 4d
<i>H. reinwardtii</i> Haw. var. <i>brevicula</i> Smith	81	Fraser's Camp, Near Fort	14	27	None	—
<i>H. reinwardtii</i> Haw. var. <i>brevicula</i> Smith	82	Fraser's Camp, 1 km E Fort	14	4	None	—
<i>H. reinwardtii</i> Haw. var. <i>huntsdriftensis</i> Smith	83	3 km E Fraser's Camp Fort	14	10	None	—
<i>H. coarctata</i> Haw.	85	Blaauw Krantz Rly. Bridge, Martindale-Grahamstown Rd	28	13	None	—
<i>H. coarctata</i> Haw.	86	Kowie River, S of White Krantz, 32 km S E Grahamstown	28	20	None	—
<i>H. reinwardtii</i> Haw. f. <i>kaffirdriftensis</i> (Smith) Bayer	88	Near Causeway on Cap Rivier, W of Kafir Drift	14	6	1 with INT. 12	3a, 4m
<i>H. reinwardtii</i> Haw. f. <i>kaffirdriftensis</i> (Smith) Bayer	89	$\frac{1}{2}$ km E of 88	14 21	5 4	None None	— —
<i>H. reinwardtii</i> Haw. f. <i>zebrina</i> (Smith) Bayer f. <i>olivacea</i> (Smith) Bayer and intermediates	90	Kafir Drift	14	26	1 with INT. 5	3c, 4g

Species	Loc. no.	Locality	2n	No. of plants studied	Chr. aberration and frequency	Fig.
<i>H. reinwardtii</i> Haw. (approaching <i>H. coarctata</i> morphologically)	91	Between Port Alfred and Southwell	28	17	2 with INT. 1A 1 with INTS. 1A and 4 3 with INT. 3 1 with INT. 3 and DEL. 2 1 with INTS. 3 and 4A 2 with DEL. 1	4b 2a, 4c 2c 4e 2b, 4f 4o
<i>H. coarctata</i> Haw.	92	Hopewell Farm, 41 km S Grahamstown on Southwell to Kenton Rd.	28	19	1 with INT. 6 1 with INT. 6 and 7	— 3b, 4h
<i>H. coarctata</i> Haw.	93	½ km S E of 92	28	7	All with INT. 8	4i
<i>H. coarctata</i> subsp. <i>coarctata</i> var. <i>tenuis</i> (Smith) Bayer	95	Harvest Vale, 12 km E Alexandria	21	6	None	—
<i>H. coarctata</i> subsp. <i>coarctata</i> var. <i>tenuis</i> (Smith) Bayer	96	½ km E of 95	14	8	2 with INT. 9	2d, 4j
<i>H. coarctata</i> Haw. (variable)	97	Salem Heights, 12 km S Salem	14	18	None	—
<i>H. coarctata</i> Haw.	98	9½ km W Vaalvley on Salem Rd.	28	7	5 with INV. 1	4n
<i>H. coarctata</i> subsp. <i>adelaidensis</i> (von Poelln.) Bayer	100	2 km N Grahamstown on Cradock Road	14	11	None	—

Species	Loc. no.	Locality	2n	No. of plants studied	Chr. aberration and frequency	Fig.
<i>H. coarctata</i> subsp. <i>adelaidensis</i> (von Poelln.) Bayer	101	6 km N Grahamstown, north of airfield	14	10	None	—
<i>H. coarctata</i> subsp. <i>coarctata</i> var. <i>greenii</i> (Baker) Bayer	102	Howiesonspoort, Ridge opposite Nature Reserve	28	5	None	—
<i>H. coarctata</i> subsp. <i>coarctata</i> var. <i>greenii</i> (Baker) Bayer	103	Howiesonspoort. At Bridge	28	13	1 with INT. 10 1 with INT. 11 1 with DEL. 3	3d. 4k 3e. 4l 4p
<i>H. coarctata</i> subsp. <i>coarctata</i> var. <i>greenii</i> (Baker) Bayer	104	Howiesonspoort. River cliff	28	2	1 with DEL. 3	4p
<i>H. reinwardtii</i> aff. f. <i>chalumensis</i> (Smith) Bayer	Bayer 91	Wesley	14	3	None	—
<i>H. reinwardtii</i> f. <i>chalumensis</i> (Smith) Bayer	Bayer 85-90	Chalumna area	21 28	47 98	Many. See Brandham (1974), Cutler (1978a)	—
<i>H. coarctata</i> Haw.	Bayer s.n.	Rooidrif	42	1	None	—
<i>H. glauca</i> Bak.	117	Between Uitenhage and Steyterville	42	10	1 with 2n = 40 1 with 2n = 43	—
<i>H. glauca</i> var. <i>herrei</i> f. <i>armstrongii</i> (von Poelln.) Bayer	112	9 km N E of Uitenhage	35	8	None	—

Cytological Methods

Somatic chromosomes were prepared from actively elongating root tips which were collected in the summer months when plants were growing the most quickly. Optimum root growth was found about 2–3 days after the plants were watered. Root tips were pretreated in saturated aqueous alpha-bromonaphthalene for 24 hours at 4 °C, fixed in 1:3 acetic alcohol, hydrolysed in normal hydrochloric acid at 60 °C for 7 minutes and stained in Feulgen using a standard technique. Squash preparations of the stained root tips were made permanent, using the liquid CO₂ method of Bowen (1956) and are kept in the collection of the Cytogenetics section of the Jodrell Laboratory as reference material. Photographs of chromosomes were taken on a Zeiss photomicroscope and drawings were made with the aid of a Wild drawing attachment at an original magnification of $\times 3000$

Anatomical Methods

The methods of preparation for scanning electron microscope (S.E.M.) studies were as in Cutler (1979). Photographs were taken in a JEOL JSM 35 instrument at 18 KeV at a constant tilt of 30°. The leaf surfaces were photographed with the long axis either vertical or horizontal with respect to the page. Prints were selected from these to show the relief to the best advantage. Selected photographs are reproduced here mostly at a magnification of c. $\times 300$ with a small number at c. $\times 40$ or $\times 660$.

For light microscope studies FAA-fixed material was washed and sectioned at c. 25 μm , stained in safranin and haematoxylin as in Cutler (1978b) and permanent slides were prepared.

Cell sizes were compared by counting the number of cells present in a standard area. Allowances were made when more than one stoma were present in the standard area.

CYTOLOGICAL RESULTS

Karyotype Structure and Chromosome Number

The basic karyotype (i.e. excluding structural chromosome mutations such as interchange) found in all plants was typical of that which occurs throughout the *Aloineae*, a tribe which is almost unique in the plant kingdom in the uniformity of its chromosome pattern. The karyotype is markedly bimodal, with diploids having $2n = 14$ chromosomes. Four pairs are long and three pairs are much shorter, about a third of the length of the long ones. The short chromosomes are difficult to distinguish from each other and no attempt will be made to do so here. They are all acrocentrics, and have a characteristic constriction in the mid-point of the long arm. This is not a secondary constriction in the generally-accepted sense (i.e. nucleolar-organising), but is simply a narrower segment

which could be heterochromatic, since it can be enhanced by cold treatment (Riley and Majumdar, 1979). Differential staining of *Aloineae* chromosomes has been achieved by Ghosh and Roy (1977), using giemsa, but we have not been able to repeat their results.

The four pairs of long chromosomes can also be classified as acrocentrics, although the short arms of some are quite substantial. They are identified as follows: The L_1 has the longest short arm and is always readily recognised. The L_2 is the longest overall and has a constriction in the short arm similar to that in the long arm of the short chromosomes. The L_3 and L_4 are somewhat similar to each other, but the L_4 is shorter and usually has the shortest short arm.

In the *Aloineae* as a whole the most frequent level of ploidy is the diploid (Brandham, 1971). Nevertheless, polyploids are common in some sections of *Haworthia*, in particular that section which is the subject of this investigation, the *Coarctatae* (Brandham, 1971, 1974). The chromosome number of every plant examined here is given in Table 1, which also includes a summary of the findings of our earlier work on triploid and tetraploid *Haworthia reinwardtii* f. *chalumensis* (Brandham, 1974; Cutler, 1978a).

Of the 26 localities that were sampled 16 contained *H. coarctata*, eight contained *H. reinwardtii* and two, *H. glauca*. Of the eight populations of *H. reinwardtii* seven were diploid ($2n = 14$), although one of these also contained triploids ($2n = 21$). Triploid individuals have been recorded previously as occurring sporadically in diploid populations of several other members of the *Aloineae*. These are usually autotriploids, and are formed directly by diploids as a result of the fusion of a non-reduced gamete with a normal one (Brandham, 1971; Abraham and Prasad, 1979).

Only one of the eight populations of *H. reinwardtii* was tetraploid ($2n = 28$), and interestingly this population (from locality 91, see Fig. 1) approached *H. coarctata* morphologically (Bayer, pers. comm.). Farther east, *H. reinwardtii* becomes exclusively polyploid, the variety *peddiensis* Smith being triploid and the forma *chalumensis* being triploid or tetraploid in all its known localities east of Wesley (Brandham, 1974).

Polyploidy is much more common in *H. coarctata*, with plants from 10 of the 16 sampled localities being tetraploid, and a single plant from one locality, Rooidrift, being hexaploid ($2n = 42$). Four of the 16 localities contained diploid plants of this species (localities 96, 97, 100, 101) and locality 95 apparently contained only triploids.

Triploids either are sterile or they produce other than eu-triploid seed progeny when selfed or crossed with each other, the possible range of chromosome number extending from diploid to tetraploid via a large number of aneuploids (Johnsson, 1942). As there is no deviation from triploidy at locality 95 it is quite probable that the population is composed entirely of a single clone spreading vegetatively, although some anatomical variability between individuals of this

population was noted (see below). Other evidence establishes the existence of two other clonal populations among the 26 populations studied (localities 93 and 112, see below).

Of the two sampled populations of *H. glauca* one comprised mostly hexaploid individuals with $2n = 42$ chromosomes (locality 117), but two of the ten individuals examined were aneuploids with $2n = 40$ or 43. Aneuploidy at this frequency is to be expected in populations of sexually-reproducing high level autopolyploids.

The other population of this species, *H. glauca* var. *herrei* f. *armstrongii* (syn. *H. armstrongii* von Poelln.) was collected from its type locality (no. 112), which is the only station where the taxon is known to occur (Bayer, 1976). All sampled plants were pentaploid ($2n = 35$), which again indicates that the population is a single clone. Bayer (1976) suggested that the taxon could be of hybrid origin, and this chromosome number confirms the idea.

Pentaploidy can arise naturally by any one of a number of routes. The most obvious of these are tetraploid \times hexaploid hybridisation, or (much less likely in *Haworthia*) octoploid \times diploid, but there are others which involve the fusion of normal gametes with non-reduced ones (i.e. those having the same chromosome number as that of the plant in which they arise, a result of meiotic failure). Pentaploids produced in this way can arise from crosses between tetraploid and non-reduced triploid or between diploid and non-reduced tetraploid.

All of the four pathways given here for the formation of pentaploids involve the crossing of plants with different ploidy levels, so it is very probable that the majority of naturally-occurring pentaploids are allopolyploids of hybrid origin. As far as *H. glauca* var. *herrei* f. *armstrongii* is concerned the present extent of our knowledge of the morphology and ploidy levels of nearby populations of *Haworthia* spp. is insufficient to allow determination of the precise parentage of this taxon, although it will be noted below that it has close affinities with tetraploid *H. coarctata*.

Chromosome Mutations

Fourteen chromosome interchanges have been found in the *Coarctatae* studied in this investigation, also at least one deletion (possibly three), and one pericentric inversion. In the diploids all mutations were heterozygous, and in tetraploids they were in the simplex heterozygous condition, i.e. having only a single morphologically altered chromosome in the case of deletions and inversions and only two altered chromosomes in each interchange. This is in common with the great majority of reported cases of chromosome interchange, both in *Haworthia* and in the rest of the *Aloineae* (Riley, 1968; Riley *et al.*, 1967; Riley and Majumdar, 1968; Brandham, 1974).

Full homozygosity for interchanges has never been found in wild-collected plants of any taxon in the *Aloineae*, and the duplex heterozygote in tetraploids

(i.e. with two pairs of altered chromosomes per interchange) has been observed in only a very few individuals in a single population of *H. reinwardtii* f. *chalumensis* (Brandham, 1974). There is also one record of a duplex deletion heterozygote in tetraploid *Aloe elgonica* (Brandham and Johnson, 1977a).

The frequency and distribution of the various mutations found in the present study are given in Table 1 and a description of each one follows. They are numbered in the order in which they were discovered. All occurred either in diploids or tetraploids, no structural chromosome mutation being found among the triploids, pentaploids or hexaploids.

Interchange 1: in *H. coarctata* subsp. *adelaidensis* (4x), loc.72. Breaks have occurred in the long arms of an L_1 and an L_3 chromosome and distal segments of unequal lengths have been exchanged to give a longer L_1 and a shorter L_3 (Fig. 4a).

Interchange 1A: in *H. reinwardtii* (4x), loc.91. This interchange is almost identical to interchange 1, with again a longer L_1 and a shorter L_3 resulting. Nevertheless interchanges 1 and 1A cannot be the same mutation because they occur in different taxa growing a considerable distance apart. The difference was confirmed by measurement of the long arms of the interchange chromosomes. In interchange 1 the shorter long arm is less than half the length of the longer, the mean ratio of length being 1:2.13, and in interchange 1A it is more than half (mean ratio 1:1.86). Interchange 1A was found alone in two individuals (Fig. 4b) but was associated with interchange 4 in a third individual from the same locality (Figs 2a, 4c).

Interchange 2: in *H. coarctata* subsp. *adelaidensis* (4x), loc.72. This is a centric fusion type of interchange with breaks at the centromere of an L_1 chromosome and one of the short chromosomes. The short arm of the L_1 and the long arm of the short chromosome have reunited to produce a metacentric which is somewhat longer than the normal short chromosomes. The long arm of the L_1 and the short arm of the short chromosome have united to produce a long chromosome which is difficult to distinguish from the normal L_3 or L_4 chromosomes (Figs 3f, 4d).

Interchange 3: in *H. reinwardtii* (4x), loc. 91. Here breaks have occurred near the centromeres of an L_3 and an L_4 chromosome with reunion of the long arms producing a very long metacentric and of the short arms, producing a short acrocentric (Fig. 2c). Because the longer arm of the short interchange chromosome is longer than the short arms of either the L_3 or the L_4 it is evident that it must also contain the proximal segment of a long arm. It is therefore apparent that the breaks involved in this interchange are not through the centromere but are proximal in the long arm of the L_3 and the short arm of the L_4 respectively. At locality 91 interchange 3 occurs either alone (Fig. 2c) or with deletion 2 (Fig. 4e) or with interchange 4A (Figs 2b, 4f).

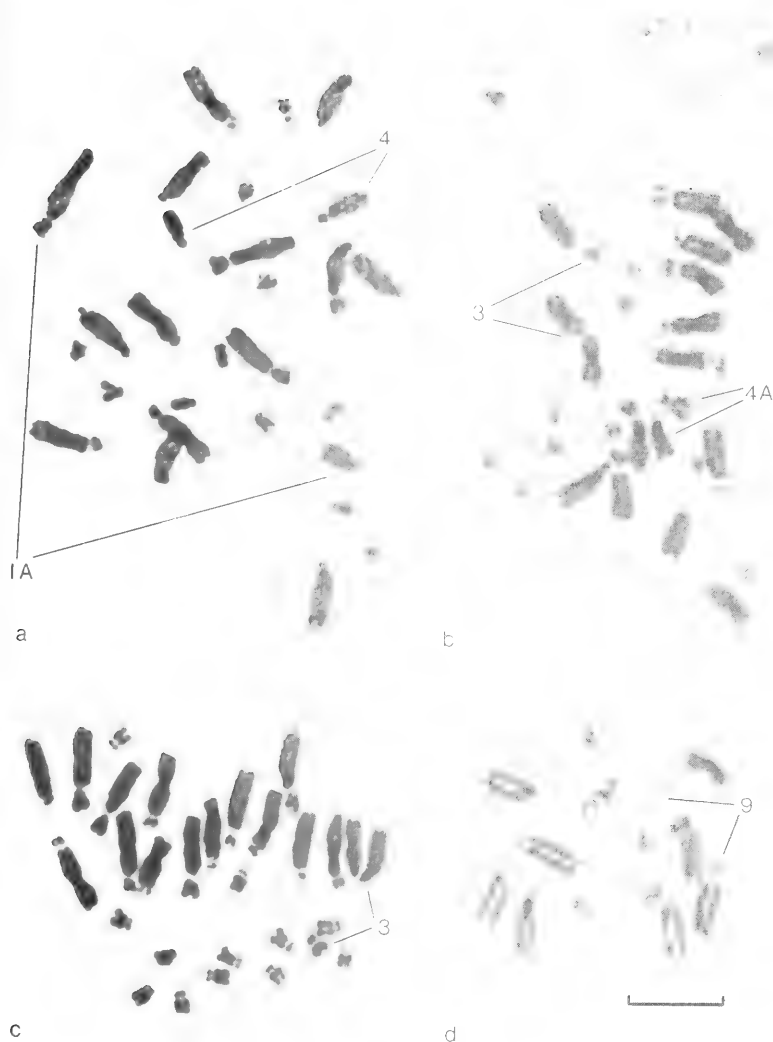


FIG. 2.

Somatic chromosomes of interchange heterozygotes. Scale = 10 μ m. a: INTS. 1A and 4 (loc. 91). b: INTS. 3 and 4A (loc. 91). c: INT. 3 (loc. 91). d: INT. 9 (loc. 96). The identity of the plants at localities numbered in Figs 2, 3 and 4 is given in Table 1.

Interchange 4: in *H. reinwardtii* (4x), loc. 91. Breaks have occurred in the long arms of an L_4 and a short chromosome, with reunion to produce two chromosomes of intermediate and almost equal length. This exchange was found in a single plant which also contained interchange 1A (Figs 2a, 4c).

Interchange 4A: in *H. reinwardtii* (4x), loc. 91. This is similar to interchange 4, but with an L_2 and a short chromosome being involved. The two interchange chromosomes are again of intermediate length, but one is considerably longer than the other (Figs 2b, 4f). Interchange 4A was also found in a single plant only, being associated with interchange 3.

Interchange 5: in *H. reinwardtii* (2x), loc. 90. This interchange involves an L_2 and an L_4 chromosome and results in the production of a very long metacentric and a very short one (Figs 3c, 4g). Normal L_2 chromosomes have a constriction (not a nucleolar-organiser) in the short arm. This constriction can be seen in the long metacentric in some favourable cells, indicating as in interchange 3 that the break points are not through the centromeres but are located proximally in the short arm of the L_2 and the long arm of the L_4 .

Interchange 6: in *H. coarctata* (4x), loc. 92. This results from breaks in the short arm of an L_1 and near the distal end of the long arm of an L_2 with reunion to produce a longer L_1 short arm and a shorter L_2 long arm (Figs 3b, 4h). This interchange was found alone in one plant and associated with interchange 7 in another.

Interchange 7: in *H. coarctata* (4x), loc. 92. Two short chromosomes are involved in this exchange. Breaks have occurred at the centromere with reunion to produce a very short metacentric derived from the two short arms and a metacentric derived from the long arms. This is a little longer than a normal short chromosome (Figs 3b, 4h). This interchange was found in only one plant, which also carried interchange 6.

Interchange 8: in *H. coarctata* (4x), loc. 93. A large segment of an L_2 long arm has been exchanged for the distal portion of the long arm of a short chromosome to produce a short interchange chromosome a little longer than a normal short chromosome and a longer interchange chromosome similar in length to many long chromosomes. The latter carries a proximal constriction on the long arm which is the equivalent of the constriction often seen in the long arm of the short chromosomes, and enables the break points to be determined precisely (Fig. 4i). Every plant sampled from locality 93 was a simplex heterozygote for this mutation, indicating either that this situation is positively selected in seed production or that the entire population is a single clone. Although the former alternative cannot be excluded until confirmatory breeding experiments are carried out, it would seem that the latter (clonal) alternative is the more likely, especially when it is recalled that a) this entire group of *Haworthia* is capable of spreading vegetatively by means of creeping and branching stems, and b) it has

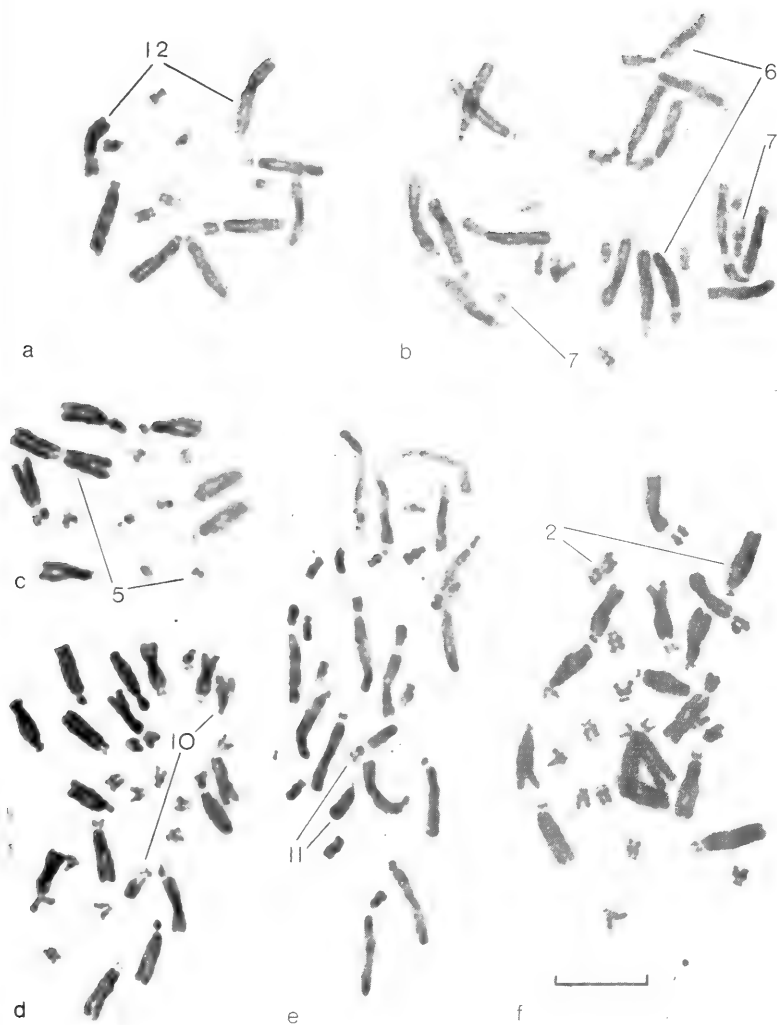
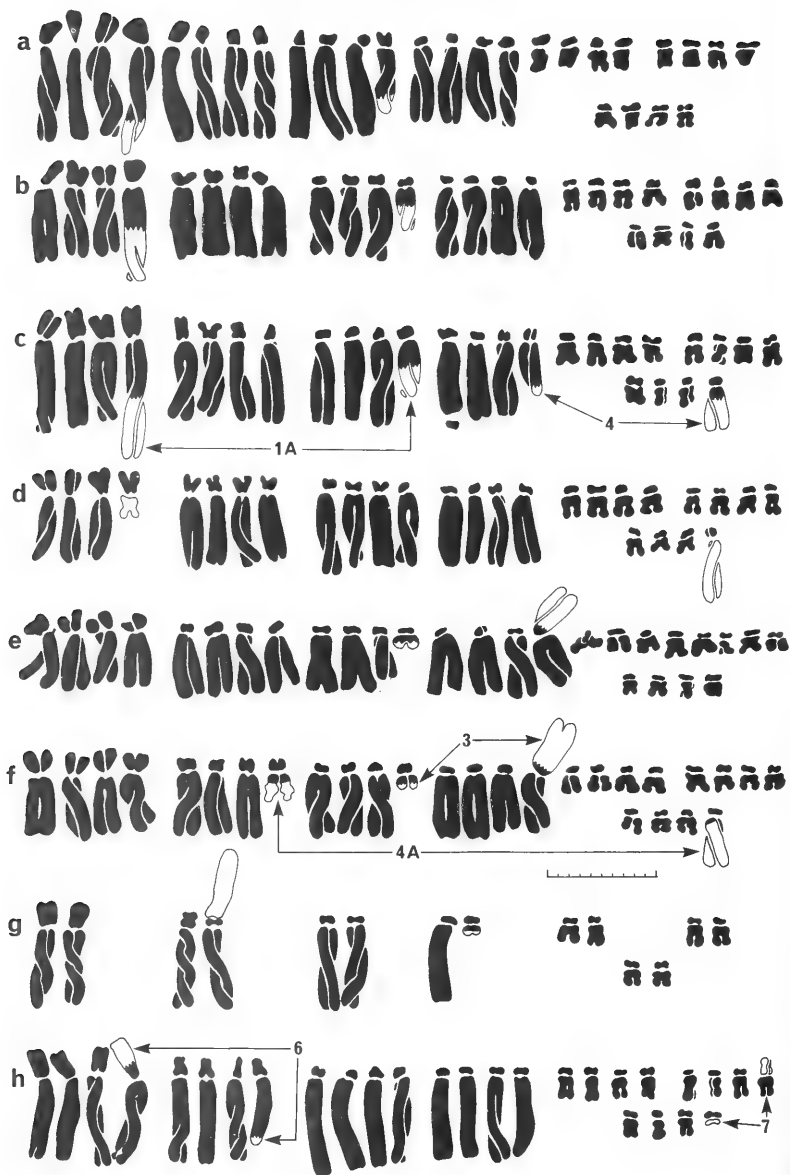


FIG. 3.
Somatic chromosomes of interchange heterozygotes. Scale = 10 μ m. a: INT. 12 (loc. 88).
b: INTS. 6 and 7 (loc. 92). c: INT. 5 (loc. 90). d: INT. 10 (loc. 103). e: INT. 11 (loc. 103).
f: INT. 2 (loc. 72).



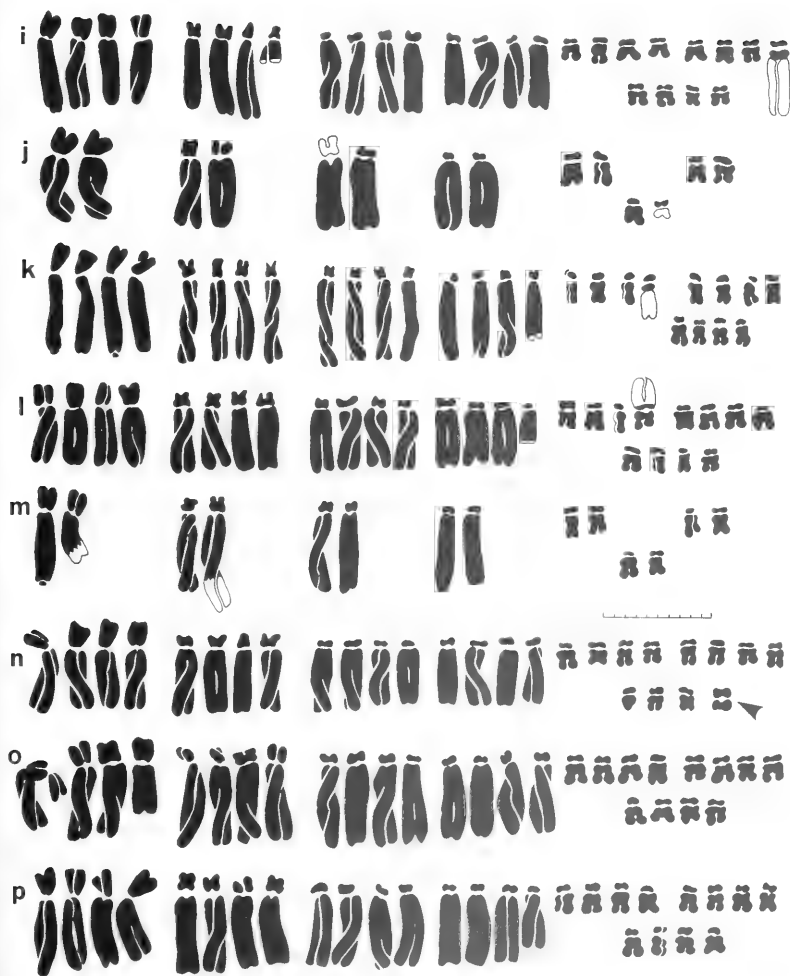


FIG. 4.

Diploid and tetraploid karyotypes showing 18 structural chromosome mutations found in *Haworthia* sect. *Coarctatae*. Interchanged chromosome segments are left unshaded for clarity. The boundary between each one and the rest of the chromosome is straight if the position of the break point is known and irregular if not precisely known. Deletions are shown by the missing portions being dotted. Scale = 10 μ m. a: INT. 1 (loc. 72). b: INT. 1A (loc. 91). c: INTS. 1A and 4 (loc. 91). d: INT. 2 (loc. 72). e: INT. 3 and DEL. 2 (loc. 91). f: INTS. 3 and 4A (loc. 91). g: INT. 5 (loc. 90). h: INTS. 6 and 7 (loc. 92). i: INT. 8 (loc. 93). j: INT. 9 (loc. 96). k: INT. 10 (loc. 103). l: INT. 11 (loc. 103). m: INT. 12 (loc. 88). n: INV. 1, a pericentric inversion giving a centromere shift (arrow) on a short chromosome (loc. 98). o: DEL. 1 (loc. 91). p: DEL. 3 (loc. 103). The identity of the plants at each locality is given in Table 1.

already been shown that another population of *H. coarctata* (at loc. 94) is also probably a clone, all specimens sampled being triploid.

Interchange 9: in *H. coarctata* subsp. *coarctata* var. *tenuis* (2x), loc. 96. This is a case of the breakage at the centromeres of an L_2 and a short chromosome. The two short arms have reunited to produce a very short submetacentric and the two long arms have joined to produce a long chromosome which is a little longer than normal. It resembles the L_1 chromosomes but can be distinguished from them by the constriction in the mid-point of its short arm, which is characteristic of the long arm of most short chromosomes (Figs 2d, 4j).

Interchange 10: in *H. coarctata* subsp. *coarctata* var. *greenii* (4x), loc. 103. Breaks have occurred at the constriction in the long arm of a short chromosome and at about three-quarters of the distance from the centromere to the end of the long arm of an L_4 chromosome. Exchange of segments gives two interchange chromosomes of intermediate length (Figs 3d, 4j).

Interchange 11: in *H. coarctata* subsp. *coarctata* var. *greenii* (4x), loc. 103. In this exchange a large portion of the long arm of an L_4 chromosome has been transferred onto the short arm of a short chromosome (Fig. 3e). It is not possible for the transferred fragment to join onto the telomere of the short chromosome's short arm, because the latter is a stable "healed" structure with which other chromosome material cannot normally fuse. Therefore there must have been a break either within that short arm or through the centromere. It is significant that in this exchange the break in the L_4 chromosome is patently not through the centromere and it has been pointed out (Brandham, 1974) that in a chromosome interchange if one break is not at the centromere the other also cannot be through the centromere. Thus the break in the short chromosome is interstitial in the short arm, even though this region is very short indeed, and the interchange has been drawn in this way in Fig. 4l.

Interchange 12: in *H. reinwardtii* f. *kaffirdriftensis* (2x), loc. 88. This is a simple exchange of different-sized portions of the long arms of an L_1 and an L_2 chromosome and results in a shorter L_1 and a longer L_2 (Figs 3a, 4m).

Inversion 1: in *H. coarctata* (4x), loc. 98. In five plants out of seven sampled from the site one of the short chromosomes was metacentric, although its length was unchanged. The remaining 27 chromosomes were apparently normal, so the plants are provisionally considered to be simplex heterozygotes for an asymmetrical pericentric inversion which has resulted in a shift in the position of the centromere (Fig. 4n). The existence of this inversion cannot be proved until meiotic and/or breeding studies confirm whether or not the characteristic phenomena associated with such inversions occur, in particular the formation of the duplicate/deletion chromosomes which are visible at AI or MII or meiosis in these plants and which sometimes survive in their progeny (Brandham and Johnson, 1977b).

Deletion 1: in *H. reinwardtii* (4x), loc. 91. In two plants sampled from this locality one of the L_1 chromosomes was considerably shortened. No other chromosome was correspondingly longer than normal, so a balanced interchange can be ruled out. In the absence of other evidence it seems that a deletion has occurred, with the loss of the distal portion (Fig. 4o). Deletions of this type are probably lethal in diploids, but have been recorded previously in triploid and tetraploid *Aloineae*, occurring both in natural populations (Brandham and Johnson, 1977a) and in the cultivated progeny of normal plants (Brandham and Cutler, 1978).

Deletion 2: in *H. reinwardtii* (4x), loc. 91. At this locality one plant contained interchange 3, and additionally an L_3 chromosome which was somewhat shorter than normal (Fig. 4e). This is apparently another simple deletion since there is not a fourth abnormal chromosome in the plant to compensate for the loss. However, reference to Table 1 will reveal that this population also contains interchange 1A (Figs 4b, 4c) in which the shorter interchange chromosome is an apparently shortened L_3 . Thus it is quite possible that the "Int 3, Del 2" plant contains interchange 3 and one only of the two chromosomes of interchange 1A, inherited as an unbalanced, though viable, gamete from one of its parents.

Deletion 3: in *H. coarctata* subsp. *coarctata* var. *greenii* (4x), loc. 103. As in the previous case this plant has a single chromosome shorter than normal, an L_4 (Fig. 4p), but again it should be noted from Table 1 that the population also contains interchange 10 (Fig. 4k), in which one of the affected chromosomes resembles a shortened L_4 . It is thus quite likely that the deletion heterozygote figured in Fig. 4p is another unbalanced interchange heterozygote carrying only one of the two altered chromosomes of interchange 10, the other being replaced by a normal one.

ANATOMICAL RESULTS

Leaf Surface Anatomy

The leaf surface anatomy typical of the complexes *H. reinwardtii* and *H. coarctata* will be described first. These will be followed by notes on the surface features of plants from all localities indicated in Figure 1 and Table 1. Selected photographs show the range of variability which occurs, and specific examples of plants of significance. Figure 5 shows cross-sections of stomata of a number of plants. It illustrates the relationship of lobes, subsidiary cells and guard cells and assists with the interpretation of the SEM photographs.

(a) The "*H. reinwardtii*" type (Figs 5a, 5c, 6)

Epidermal cells are 4-5-6-7 sided, normally slightly longer than wide. The position of the anticlinal walls is indicated by shallow, narrow grooves. Epidermal cell outer walls are convex to a greater or lesser degree and in some examples from the eastern end of the range of the species they are produced

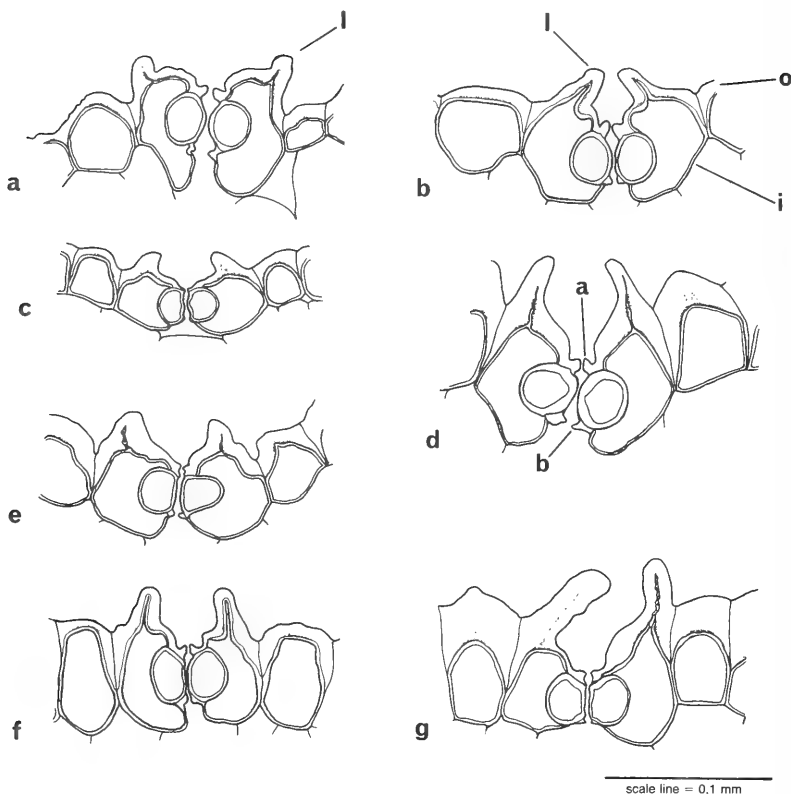


FIG. 5.

Transverse sections through stomata and adjacent epidermal cells. Scale = 100 μm . a: *H. reinwardtii* forma *chalumnensis* (73–1007, tetraploid). Note position of lateral lobes of rim to suprastomatal cavity (l). b: *H. coarctata* (loc. 98, tetraploid.) Note overarching lateral lobes of rim to suprastomatal cavity. c: *H. reinwardtii* var. *huntsdriftensis* (loc. 83, diploid). Similar to a above but its cells are smaller. d: *H. glauca* var. *herrei* forma *armstrongii* (loc. 112–1279, pentaploid). This plant has a stomatal structure similar to that of *H. coarctata* in b above, but all cells are larger. e: *H. coarctata* subsp. *coarctata* var. *tenuis* (loc. 96, diploid). This plant has stomata reminiscent of *H. reinwardtii* s.l.. f: *H. coarctata* subsp. *coarctata* var. *tenuis* (loc. 95, triploid). This plant shows stomata with a tendency towards the type found in *H. coarctata*. g: *H. glauca* (loc. 117–1325, hexaploid). This plant has long and irregular lobes surrounding the suprastomatal cavity but is otherwise like *H. coarctata*.

In the diagrammatic representation of the sections above, at o, the outer part of the epidermal cell wall and cuticle are not drawn separately. The cuticle is relatively thin, but the outer wall is extensively cutinized. Some granular inclusions are shown but the clearly stratified nature of this outer part of the wall is not indicated, for the sake of clarity. The thinner, inner part of the cell wall, i, is not impregnated with cutin and takes up safranin in the preparations, whereas the outer part of the wall remains clear. The stomata have outer (a) and inner (b) cuticular ledges developed to a greater or lesser degree.

into a conical, more or less central papilla. A sculpturing of micropapillae is evident. This is composed of cell wall and cuticle. *Stomata* are deeply sunken. The outer cuticular rim is visible from above, but the regulated aperture is difficult to see except in T.S. The most prominent feature is the raised rim composed of four lobes, one from each of the cells adjacent to the guard cells (subsidiary cells). The lobes are ridges of outer wall, accentuated by cuticle, arising along the long axis of flanking cells and across the width of the polar cells. On the flanking cells the ridge arises along the centre of the wall; away from the stoma the outer part of the wall bears micropapillae which are normally larger than those on other epidermal cells, but towards the guard cells the outer wall is more or less smooth and slopes gently inwards. On the polar cells the lobes arise from the outer wall along the side nearest to the guard cells. The outer aperture defined by the lobes is rectangular with the long axis parallel to the long axis of the leaf. The lobes are upright to slightly overarching.

Wax is present as a continuous thin sheet and as sparse crystals in the form of flakes or as larger irregular particles

(b) The "*H. coarctata*" type (e.g. Figs 5b, 5e, 5f, 7)

Very similar in many respects to the "*H. reinwardtii*" type but *epidermal cells* exhibit a wider range of sculpturing, and in many specimens the micropapillae are more pronounced. Larger central papillae are a common feature. Anticlinal wall position is sometimes related to narrow bands of unsculptured surface around cells. The most conspicuous differences relate to the *stomata*. The guard cells are deeply sunken, and the outer cuticular rim can normally be seen only with difficulty from above because the thick lobes forming the rim are normally strongly overarching. The lobes on the flanking cells are set towards the edge of the cell nearest the guard cell pair. This together with the fact that the part of the outer wall nearest to the guard cells slopes steeply inwards gives a characteristic appearance to the stomatal apparatus.

Wax is as in the "*H. reinwardtii*" type

(c) Individual descriptions of plants from each locality

The main differences of significance relate to stomatal structure, principally the subsidiary cell lobing. The individuals described here are selected from the range of material studied from each locality and are representative of that locality. Where the individuals differ widely at a particular locality, the range of variation is described. This is most marked where there are differences of ploidy level. Descriptions of epidermal cell structure refer to outer walls only.

It may be assumed that micropapillae on subsidiary cells are coarser than those on normal epidermal cells, unless otherwise stated.

Loc. 71: *H. coarctata*, 4x (Fig. 7a); *Epidermal cells* with strongly domed outer walls; cuticular sculpturing composed of micropapillae showing some tendency towards aggregation into irregular ridges radiating from centre of cell. *Stomata* with very strongly overarching lobes, outer pore small, with square outline.

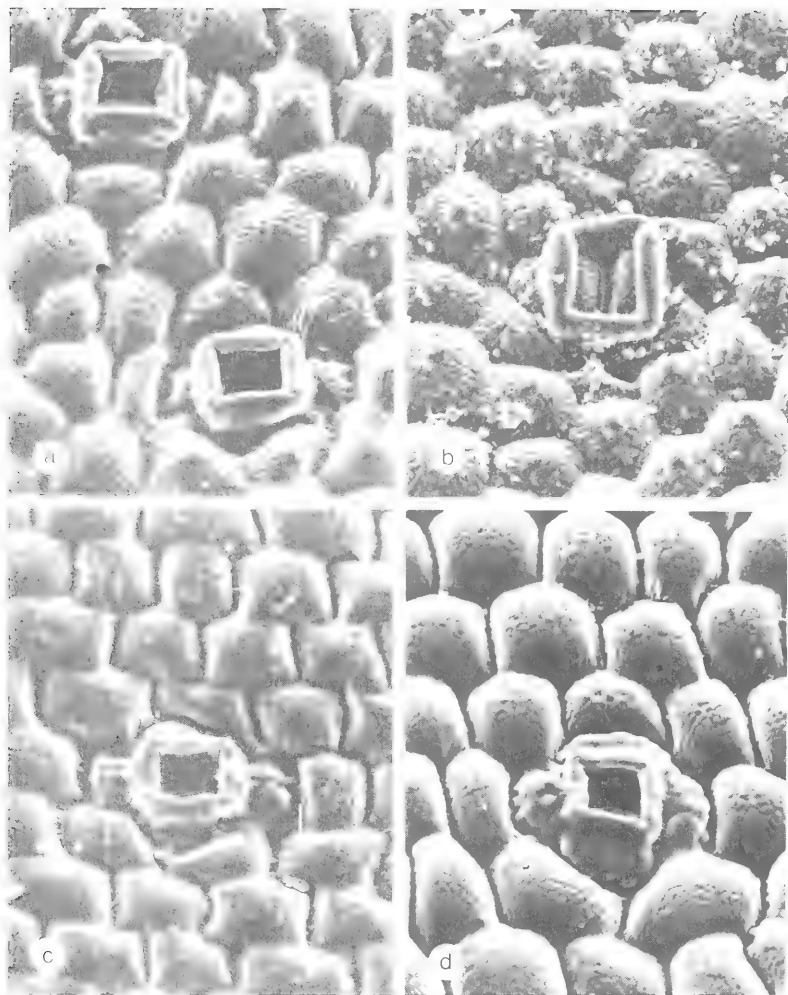


FIG. 6.

Leaf epidermis of *H. reinwardtii*. All show the typical "reinwardtii" type of stomata. a: *H. r.* forma *kaffirdriftensis*, loc. 88–945 (diploid). b: *H. r.* aff. forma *chalumnensis* from Wesley (diploid). The conspicuous particles are wax. c: *H. r.* forma *kaffirdriftensis*, loc. 89–955 (diploid). d: *H. r.* forma *kaffirdriftensis*, loc. 89–958 (triploid). Cells are larger than those of the diploid from the same locality in Fig. 6c. All $\times c. 300$.

Loc. 72: *H. coarctata* subsp. *adelaidensis*, 4x (Fig. 11a); *Epidermal cells* subconical, with rounded central papilla equivalent to about $\frac{1}{3}$ of width of cell; sculpturing composed of micropapillae showing some tendency towards aggregation into irregular ridges radiating from central papilla. *Stomata* with very strongly over-arching lobes, outer pore small, with rectangular outline.

Loc. 81: *H. reinwardtii* var. *brevicula*, 2x; *Epidermal cells* with outer walls forming low domes; sculpturing of micropapillae showing slight tendency to random aggregation. *Stomata* with slightly incurved lobes; typical for *H. reinwardtii*, with wide rectangular outer pore.

Loc. 82: *H. reinwardtii* var. *brevicula*, 2x; *Epidermal cells* low conical, with small central papilla equivalent to about $\frac{1}{5}$ of width of cell; sculpturing composed of narrow, irregular ridges radiating from centre of cell, and occasional micropapillae. *Stomata* as for loc. 81.

Loc. 83: *H. reinwardtii* var. *huntsdriftensis*, 2x (Fig. 5c); *Epidermal cells* low conical, with or without small central papilla equivalent to about $\frac{1}{5}$ of width of cell; sculpturing composed of small, poorly defined micropapillae showing a tendency to random aggregation. *Stomata* of *H. reinwardtii* type, with wide rectangular pore, but lobes slightly over-arching.

Loc. 85: *H. coarctata*; 4x; *Epidermal cells* more or less flat (Specimen no. 85–890) or strongly domed (85–900); sculpturing composed of micropapillae showing some aggregation. *Stomata* of *H. coarctata* type, with thick, over-arching lobes and small rectangular outer pore, but outer wall of flanking subsidiary cells adjacent to guard cells only moderately inward-sloping.

Loc. 86: *H. coarctata*, 4x; As 85–900, but *stomata* with more strongly over-arching lobes, and smaller outer pore.

Loc. 88: *H. reinwardtii* f. *kaffir driftensis*, 2x (Fig. 6a); *Epidermal cells* strongly domed, some tending to conical with small central papilla equivalent to about $\frac{1}{5}$ of width of cell; sculpturing composed of micropapillae showing a little, random aggregation. *Stomata* of typical *H. reinwardtii* form but prominent since the subsidiary cells, apart from rim of pore, are lower and have micropapillae which are larger than those of other epidermal cells.

Loc. 89: *H. reinwardtii* f. *kaffir driftensis*, 89–955, 2x (Fig. 6c); *Epidermal cells* and *stomata* as for loc. 88.

Loc. 89: *H. reinwardtii* f. *kaffir driftensis*, 89–958, 3x (Fig. 6d); *Epidermal cells* larger and more strongly domed than in diploids, and *stomata* more prominent.

Loc. 90: *H. reinwardtii* f. *zebrina*, 2x; *Epidermal cells* slightly domed, sculpturing composed of micropapillae showing extensive random aggregation. *Stomata* of *H. reinwardtii* type but with more strongly over-arching lobes than normal.

Loc. 91: *H. reinwardtii/coarctata* intermediate, 4x; A very varied population; the

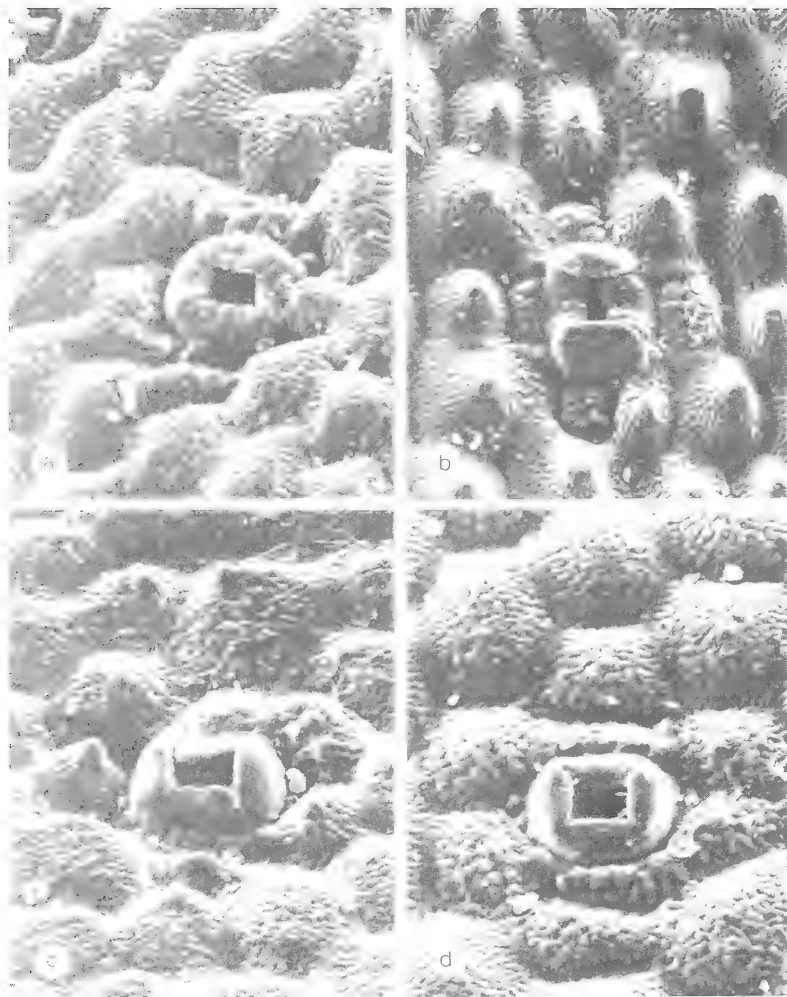


FIG. 7.

Leaf epidermis of *Haworthia* species, all with stoma types characteristic of *H. coarctata*: a: *H. coarctata*, loc. 71–687. b: *H. reinwardtii*—*H. coarctata* intermediate, loc. 91–1018. This shows an unusual feature, the lateral lobes of the stoma overarched by those of the poles. c: *H. coarctata*, loc. 92–1051. d: *H. coarctata*, loc. 93–1060. All tetraploids; all \times c. 300.

four samples described here represent two plants tending towards the anatomy of *H. reinwardtii* and two towards *H. coarctata*.

91–1013; *Epidermal cells* slightly domed; sculpturing composed of micropapillae with some aggregation. *Stomata* of *H. reinwardtii* type but with very thick lobes.

91–1017; As 91–1013 but *epidermal cells* more strongly domed.

91–1010; *Epidermal cells* strongly domed; sculpturing composed of micropapillae with some aggregation. *Stomata* of *H. coarctata* type.

91–1018 (Fig. 7b); *Epidermal cells* with wide, sculpture-free bands above anticlinal walls; central area slightly domed to sub-conical; sculpturing of fine micropapillae in most cells aggregating at centre to form small papilla c. $\frac{1}{3}$ width of cell. *Stomata* of *H. coarctata* type but with lateral lobes slightly concave and overarched by end lobes. This unusual feature might be connected with the existence of a chromosome deletion in this plant (Fig. 4o).

Loc. 92: *H. coarctata*, 4x (Fig. 7c); *Epidermal cells* slightly domed, the dome frequently flat-topped, occasionally developed into a conical papilla; sculpturing composed of moderately coarse micropapillation with some aggregation. *Stomata* of *H. coarctata* type.

Loc. 93: *H. coarctata*, 4x (Fig. 7d); *Epidermal cells* moderately domed, position of anticlinal walls indicated by bands lacking prominent sculpturing; remaining wall area with coarse micropapillae showing some aggregation.

Loc. 95: *H. coarctata* subsp. *coarctata* var. *tenuis*, 3x (Figs 5f, 8a); Two specimens described here to show variability.

95–1075; *Epidermal cells* conical with central papilla equivalent to about $\frac{1}{3}$ width of cell; sculpturing of micropapillae, coarser on papillae than on remainder of cell, tending to aggregate into ridges radiating from centre of cell. *Stomata* with thick overarching lobes, as in *H. coarctata*, but internally more like *H. reinwardtii*. The low power photograph in Fig. 8a shows a tubercle and regular distribution of stomata.

95–1080 (Fig. 8b); *Epidermal cells* domed, occasionally subconical; sculpturing consisting of moderately coarse micropapillae showing a tendency to random aggregation; some aggregation into small papillae at apex of cones equal to c. $\frac{1}{3}$ of cell width; anticlinal wall positions defined by strips with very low relief sculpturing; *stomata* tending to *H. reinwardtii* type.

Loc. 96: *H. coarctata* subsp. *coarctata* var. *tenuis*, 2x (Figs 5e, 8c, 8d); Most *epidermal cells* low domed or sub-conical, with small central papilla about $\frac{1}{3}$ of cell width; sculpturing composed of coarse micropapillae the largest fusing to form the central papilla, others tending to aggregate and form ridges radiating from cell centre; *stomata* typical of *H. reinwardtii*, but inwardly sloping areas of flanking subsidiary cells slightly undulating and ribbed.

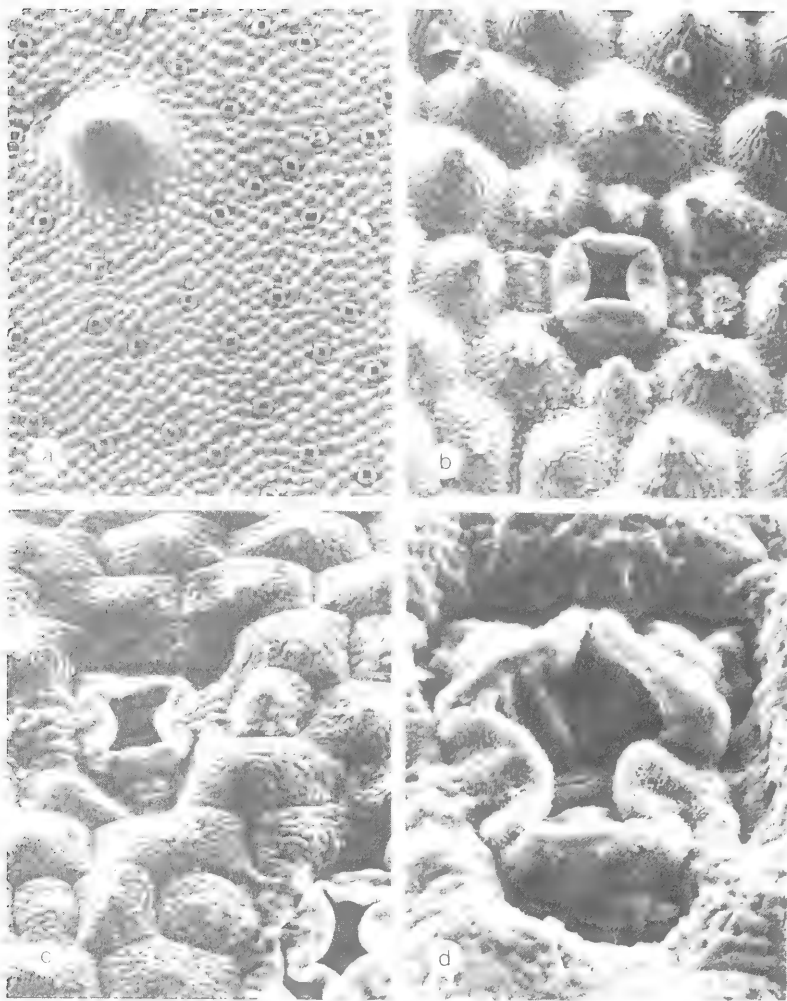


FIG. 8.

Leaf epidermis of *H. coarctata* subsp. *coarctata* var. *tenuis*. a: loc. 95-1075 (triploid). Low power photograph (\times c. 40) showing a single leaf tubercle and demonstrating the uniformity of epidermal sculpturing and stoma shape over a large area. b: loc. 95-1080 (triploid), \times c. 300. c: loc. 96-1089 (diploid) \times c. 300. d: as c, a stoma at higher magnification showing irregular stoma lobes with ridging, \times c. 660.

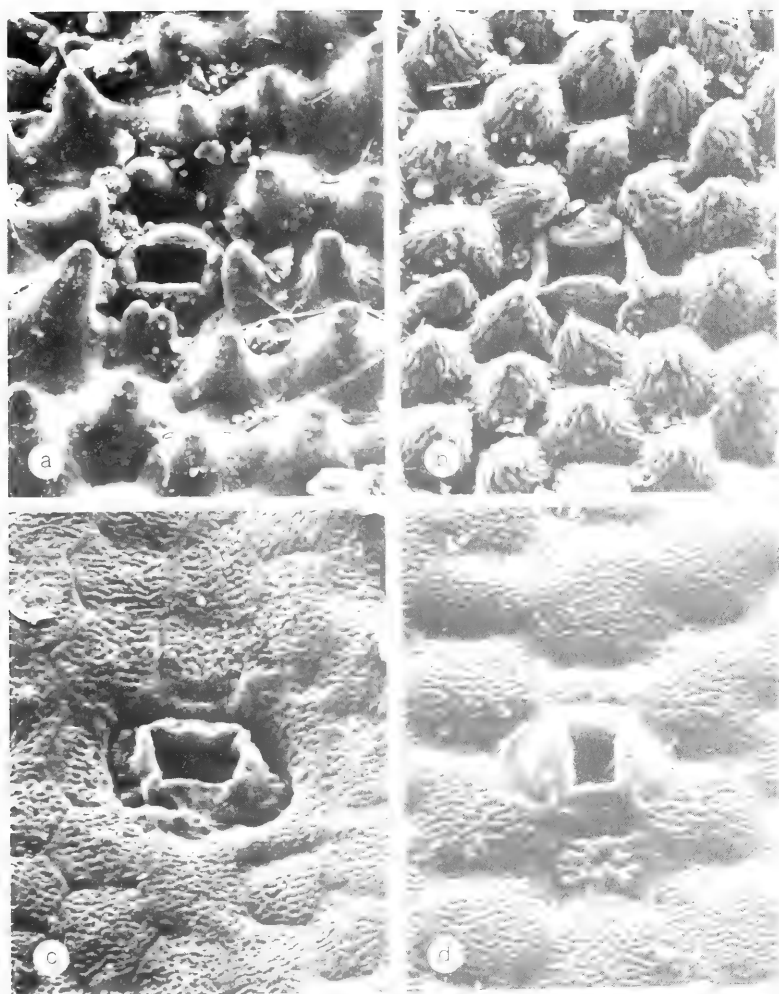


FIG. 9.

Leaf epidermis of *H. coarctata*. a, b, c: three examples of the very variable diploid population at loc. 97. a: 97-1104. b: 97-1112. c: 97-1107. d: *H. coarctata* subsp. *coarctata* var. *greenii*, loc. 103-1183 (tetraploid). All $\times c. 300$.

Loc. 97: *H. coarctata* variable, 2x (Figs 9a, b, c); No two specimens alike. Two major trends observed; the majority with very well-developed papillae arising from conical epidermal cells; others with very slightly domed epidermal cell walls. Two examples of the former type and one of the latter are described.

97–1104 (Fig. 9a); *Epidermal cells* extended into tall cones, each terminated by a small papilla equivalent to $\frac{1}{3}$ of cell width; cones adjacent to subsidiary cells curving towards stomata. Sculpturing consisting of medium-sized micro-papillae with some aggregation to form ridges radiating from cell centre (sculpturing obscured by rather thick wax layers); *stomata* most like *H. reinwardtii* type.

97–1112 (Fig. 9b); *Epidermal cells* extended into medium-sized cones each with a poorly defined central “papilla” formed by aggregation of coarse micropapillae; flanks of cone with sculpturing of coarse micropapillae aggregating into irregular ridges radiating from cell centre; cones adjacent to subsidiary cells curving towards stomata. *Stomata* of *H. reinwardtii* type but with polar lobes overarching.

97–1107 (Fig. 9c); *Epidermal cells* more or less flat or low-domed; outlines of cells clearly defined by double lines devoid of sculpturing; outer wall sculpturing composed of micropapillae finer than those of 97–1112, showing some random aggregation; *stomata* of *H. reinwardtii* type.

Loc. 98: *H. coarctata* 4x; *Epidermal cells* low domed; sculpturing composed of moderately pronounced micropapillae showing some aggregation into short irregular ridges arranged across width of the cells; *stomata* of *H. coarctata* type; guard cells not as deeply sunken as in most other specimens.

Loc. 100: *H. coarctata* subsp. *adelaidensis* 2x (Figs 10a, b, c); Specimens from this locality were variable. Epidermal cells low domed in 100–1153 (Fig. 10a), produced into small irregular cones in 100–1149 (Fig. 10b) or well-developed cones with small central papilla in 100–1143 (Fig. 10c); sculpturing of medium-sized (100–1143 and 1153) or coarse micropapillae (100–1149), with a considerable tendency to irregular aggregation in 100–1149 or to radiating ridges in 100–1143. Micropapillation not noticeably larger on subsidiary cells in 100–1143 or 100–1149 contrary to that on almost every other plant in this study; *stomata* in all samples of *H. coarctata* type.

Loc. 101: *H. coarctata* subsp. *adelaidensis* 2x (Fig. 10d); Specimens from this locality variable; 101–1161 similar to 100–1153; 101–1163 (Fig. 10d) similar to 101–1161 except for each epidermal cell bearing a small central papilla equal in diameter to about $\frac{1}{6}$ of cell width. 101–1159 resembling 100–1143 except that cells smaller.

Loc. 102: *H. coarctata* subsp. *coarctata* var. *greenii* 4x; *Epidermal cells* moderately domed; sculpturing of fine to medium micropapillae with a tendency to random aggregation; *stomata* of *H. coarctata* type.

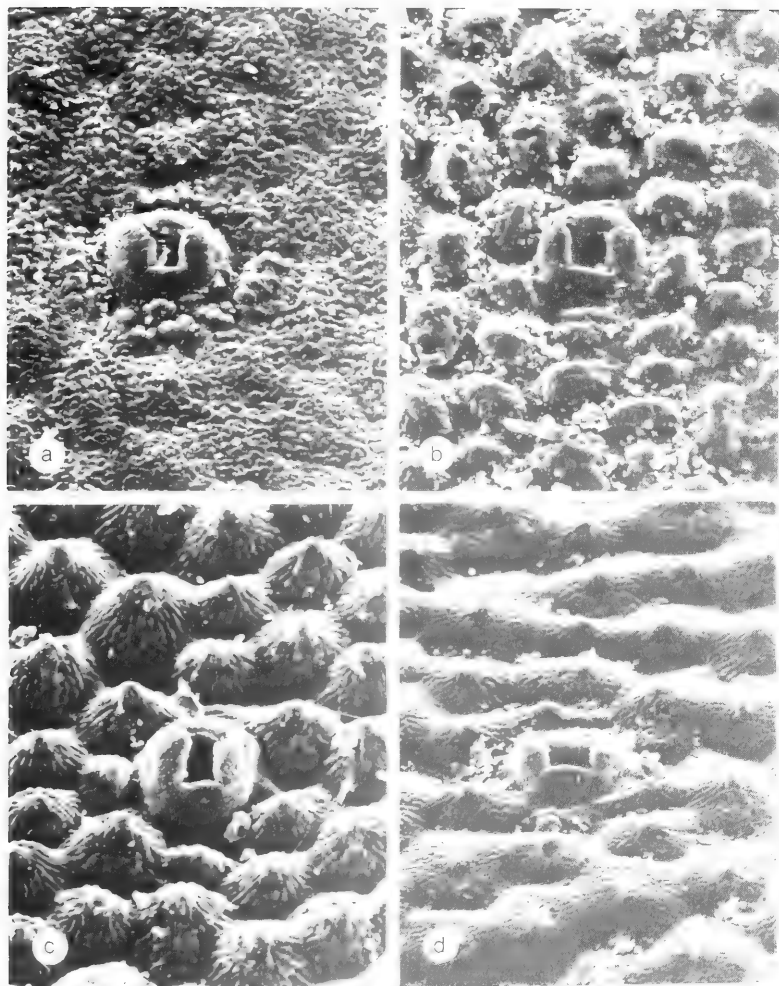


FIG. 10.

Leaf epidermis of *H. coarctata* subsp. *adelaidensis*. a, b, c: three examples of the variable diploid population at loc. 100. a: 100-1153. b: 100-1149. c: 100-1143. d: loc. 101-1163 (diploid). All \times c. 300.

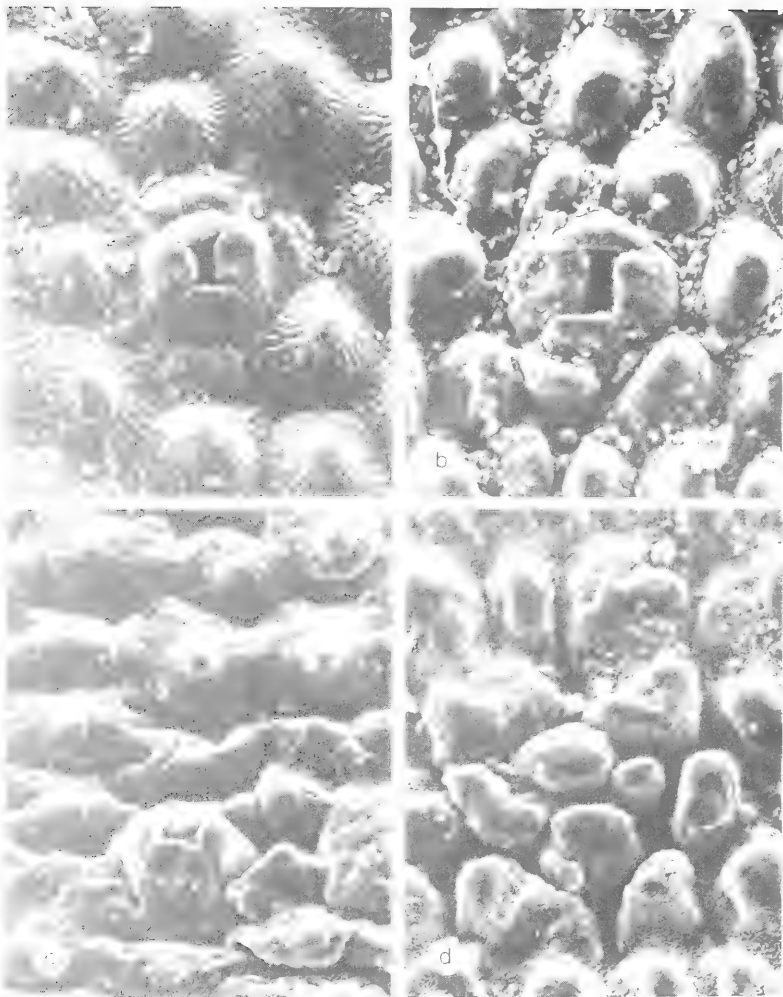


FIG. 11.

Leaf epidermis of *Haworthia* species. a: *H. coarctata* subsp. *adelaidensis*, loc. 72–707 (tetraploid) with larger cells than in diploid plants of the same subspecies (Figure 10). b: *H. glauca* var. *herrei* forma *armstrongii*, loc. 112–1277 (pentaploid). c: *H. coarctata*, hexaploid from Rooidrift. d: *H. glauca*, loc. 117–1321 (hexaploid). The suprabasilar lobes are very thick, making it difficult to determine the position of the stomata. All $\times c. 300$.

Loc. 103: *H. coarctata* subsp. *coarctata* var. *greenii* 4x; Most specimens as for loc. 102 (Fig. 9d), but one specimen with concave flanking lobes of the stoma.

Loc. 104: *H. coarctata* subsp. *coarctata* var. *greenii* 4x; 104–1196, as for loc. 102 but *epidermal cells* not so domed; 104–1197 as for loc. 102 but most *epidermal cells* with a small central papilla equivalent in diameter to $\frac{1}{8}$ – $\frac{1}{6}$ of cell width. Occasional anomalous 5-lobed *stomata* present in 104–1197.

Bayer Loc. 91: Wesley, *H. reinwardtii* aff. f. *chalmensis* 2x (Fig. 6b); *Epidermal cells* subconical, most with small central papilla with diameter equivalent to $\frac{1}{8}$ of cell width; sculpturing of moderately coarse micropapillae showing some aggregation; *stomata* prominent, of *H. reinwardtii* type.

Bayer s.n. Rooidrift, *H. coarctata* 6x; *Epidermal cells* conical with somewhat overarching anticlinal walls; most with large terminal papilla equal to $\frac{1}{4}$ – $\frac{1}{3}$ of width of cell; sculpturing of low relief coarse micropapillae obscured by wax covering; *stomata* intermediate between *H. coarctata* and *H. reinwardtii* types with somewhat irregular lobes.

Loc. 112: *H. glauca* var. *herrei* f. *armstrongii* 5x (Figs 5d, 11b); *Epidermal cells* conical, most with central papilla equivalent in diameter to $\frac{1}{2}$ – $\frac{1}{3}$ of width of cell; sculpturing of coarse, low relief micropapillae; *stomata* of *H. coarctata* type but with very thick overarching lobes bordering a small outer aperture.

Loc. 117: *H. glauca* 6x (Figs 5g, 11d); *Epidermal cells* with irregular strongly domed outer walls, each like a stubby papilla; those next to subsidiary cells curving towards stoma; sculpturing not observed; part of surface obscured by fine upright wax flakes; *stomata* with four distinct very much enlarged lobes only slightly smaller than the papillae of the adjacent cells; lobes almost closing sup-rastomatal cavity.

Ploidy level and cell size

The number of cells per unit leaf area was scored in 102 plants of all levels of ploidy from 2x to 6x. These figures, together with a conversion into relative mean cell surface area are given in Table 2.

DISCUSSION

The significance of epidermal features and polyploidy in relationships between populations

Within the *Aloineae*, the details of stomatal structure and cell wall/cuticular sculpturing have been shown to be of diagnostic, and in some instances, of taxonomic significance (Cutler, 1979). Confusion has arisen frequently regarding the identification of plants in the section *Coarctatae* of the genus *Haworthia*. In particular, *H. reinwardtii* and *H. coarctata* together with their varieties and forms are easily confused. The problems have been made worse since the plants are widely cultivated: many varieties and forms have been described from culti-

TABLE 2.
Ploidy level, cells per unit area and relative areas of individual cells.

Ploidy level	2x	3x̄	4x	5x	6x
No. of plants scored	40	7	40	6	9
Mean no. of cells per unit area	44	36	35	25	26
Relative areas of individual cells	1	1.22	1.26	1.76	1.69

vated material. The majority of taxa in this group are interfertile and undoubtedly many hybrids have arisen which are not recognised as such. Intensive selection by collectors has also provided plants for which new names have been given which are of no taxonomic significance (e.g. the many works of Resende, quoted by Bayer, 1976:177).

It was essential to return to localities in the wild to find suitable material so that a rational approach could be made to the classification of this group. Bayer (1973, 1976) has recently done this. As a result of his studies he eliminated or changed the rank of a large number of taxa. He relied heavily on morphology and distribution. The flowers provide little of significance whereby species can be identified, being extremely uniform throughout the group.

During the period that Bayer was studying these plants, we were working on the Kew collections. We recognised the need for wild-source material and were able to collaborate with him in making additional collections from sites which he showed us. We were then able to study the anatomy and cytology of the plants, mainly to see whether there was anything of taxonomic significance that could be derived from these new approaches.

The chromosome results revealed that both *H. reinwardtii* s.l. and *H. coarctata* s.l. contained diploid, triploid and tetraploid plants (also hexaploid in *H. coarctata*). This, then, provided little help with classification. The chromosome interchanges, although of considerable interest as far as chromosome mechanics are concerned (see below), similarly provide no taxonomic information because no two populations contained the same interchange. This is unlike the situation in *H. reinwardtii* f. *chalumensis* in which inter-population interchange distribution was a valuable aid to determining evolutionary trends (Brandham, 1974).

The anatomical data on their own gave some help towards an understanding of the problem, but contained apparent anomalies. On the whole, plants called *H. coarctata* by Bayer showed one type of stoma, whereas those called *H. reinwardtii* had another distinct type. There were exceptions, where plants with the general morphology of *H. coarctata* had the stomatal configuration of *H. reinwardtii*, e.g. *H. coarctata* subsp. *coarctata* var. *tenuis* at Loc. 96 (Figs 8c, d) and *H. coarctata* from Loc. 97 (Fig. 9c). Bayer included some populations of plants in *H. coarctata* because of their geographical distribution, even though

they might be mistaken for *H. reinwardtii*. These were found to have the *H. coarctata* type of stoma, e.g. *H. coarctata* var. *adelaidensis* at Locs 100 and 101 (Figs 10a, b, c, d). It was necessary to combine the cytological and anatomical approaches to make progress in clarifying this involved biological problem.

We have been able to describe here all of the cytological data, but space has restricted us to selecting only a small proportion of the anatomical information for presentation. Great care was taken to select representative plants and where variability existed in populations, to demonstrate the range.

Photographs of the leaf surfaces of the entire collection were laid out in a geographical arrangement, together with details of chromosome numbers. An attempt was made to elucidate affinities, and our results are based on those observations.

The genetic variability within this complex was reflected in leaf surface sculpturing, as we would have expected from previous studies (Brandham and Cutler, 1978).

Interchange and deletions do not on the whole seem to be detectable as consistent variations in the anatomy of these plants, as was the case in *H. reinwardtii* f. *chalumnensis* (Cutler, 1978a), but in the present study much smaller sample numbers were examined from individual populations. It is possible that there might be a detectable relationship if larger numbers could be studied. However, the abnormal stomatal structure in the *H. reinwardtii/coarctata* intermediate, no. 91–1018 (Fig. 7b) could be associated with the chromosome deletion that it carries (Fig. 4o).

Inter-population affinities

(a) *Diploids*

Four main geographically distinct groups of diploids were found (Fig. 12). It seems probable that they may be relicts of a larger population. The extensive variability which they display is not surprising in such relict groups.

The three western groups share some of the characteristics associated with *H. coarctata*, but also exhibit close links with *H. reinwardtii* to the east. The northernmost of these groups (Locs 100, 101) show morphological similarity to *H. reinwardtii* as defined by Bayer, but have the stomatal type which in this paper we associate with *H. coarctata*. Bayer has treated this group as *H. coarctata* on the basis of its distribution, since it is close to the type population of *H. coarctata* subsp. *adelaidensis* (Loc. 72).

The west-central group of diploids (Loc. 97) shows considerable variation in both morphology and leaf surface sculpturing. Because of their distribution, Bayer (1973, 1976) has included these plants with *H. coarctata*, but it can be seen from Figs 9a, b, c that they have a stomatal type reminiscent of *H. reinwardtii*.

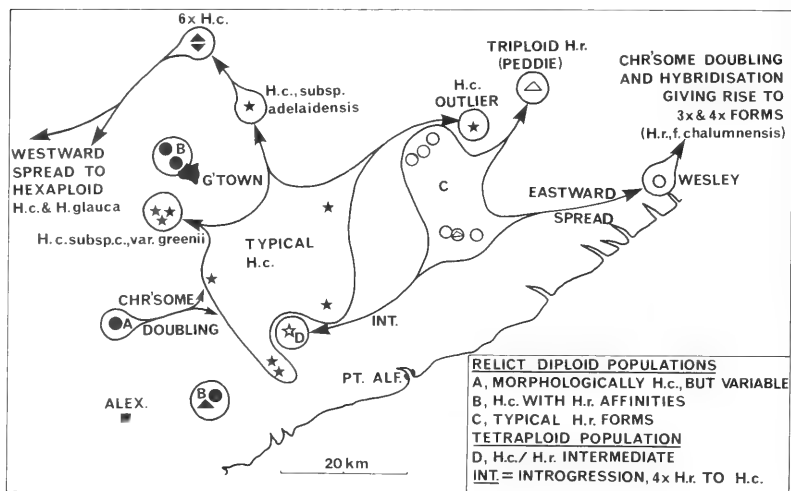


FIG. 12.

Map of the Grahamstown - Port Alfred area showing probable evolutionary trends in *Haworthia reinwardtii* (H. r.), *H. coarctata* (H. c.) and related forms. A full explanation is given in the text. Symbols are as in Figure 1.

Plants at the limit of their range of distribution are often genetically diverse and this seems to be the case here. Plants with the two extreme types of epidermal cell sculpturing illustrated by Figs 9a and 9c might be expected to produce hybrids with an intermediate type such as that shown in Fig. 9b. Controlled crossing experiments by Cutler and Brandham (1977) using other members of the *Aloineae* revealed that F_1 hybrids normally show a type of surface sculpturing intermediate between those of the parents.

The south-west group of diploids (Locs 95-96) consists of plants with a distinctive, slender form. It includes triploids of local origin (Loc. 95) which are not distinguishable from the diploids using characters of gross morphology for comparison. However, the diploids have stomata reflecting similarity with *H. reinwardtii* and the triploids show a stronger tendency to exhibit the *H. coarctata* form of stomata. It may be that the triploids are expressing a dosage effect for the *coarctata* stomatal type. Bayer calls these plants *H. coarctata* var. *tenuis*.

The major group of diploids is centred on the Fish River, as exemplified by Localities 81, 82, 83, 88, 89 and 90 in this study. Local triploids also occur at Locality 89. These plants have been grouped together by Bayer as *H. reinwardtii*. They do show some variation in both anatomy and morphology which previously has been recognised in the described varieties *brevicula* and *huntsdriften*.

sis and the forms *kaffirdriftensis*, *zebrina* and *olivacea*. However, there are no anatomical variations which correlate with any of these varieties or forms. All exhibit the *H. reinwardtii* type of stoma.

Among all diploid groups, then, there are hints, either in morphology or anatomy, of a common ancestry. Separation of the western populations as *H. coarctata* s.l. seems to be rather arbitrary.

(b) Tetraploids

There are two major groups of tetraploids. One, which is described as 'typical *H. coarctata*' by Bayer (1976), occupies a broad zone between Grahamstown and Port Alfred (Localities 85, 86, 92, 93 and 98). The other, *H. reinwardtii* f. *chalumensis* (Smith) Bayer, occurs much further east of the main diploid *H. reinwardtii* complex, at and around Chalumna. This second group was the subject of earlier papers (Brandham 1974; Cutler, 1978a). In the first of these two papers the conclusion was reached that evolution had taken place from diploids in the west to triploids and tetraploids in the east, via the diploids growing at Wesley, and our find of more diploid *H. reinwardtii* in the Fish River valley confirms this conclusion.

The western group of tetraploids is of principal concern to us in this paper. Members of this group show closest morphological affinities with the diploids to their west at Locality 97 near Salem. We suggest, therefore, that they could have arisen by chromosome doubling in diploids from this area.

This western group of tetraploids appears to be expanding territorially in several directions. There is an eastern outlier at Locality 71, Huntsdrift, a western outlier with some morphological differentiation (described as *H. coarctata* subsp. *coarctata* var. *greenii* (Baker) Bayer) at Howiesonspoort, Localities 102, 103 and 104, and a northern form at Locality 72, Queens Road, NE of Grahamstown, which is slightly smaller, and is called *H. coarctata* subsp. *adelaidensis* (von Poelln.) Bayer. All of these plants show the typical '*H. coarctata*' type of stoma, with some slight variations in epidermal cell cuticular sculpturing.

A particularly interesting population of tetraploids is found at Locality 91. Bayer (pers. comm.) described these plants as intermediate between *H. reinwardtii* and *H. coarctata*. The population is cytologically very unstable, with six mutant karyotypes (Table 1) in addition to plants with apparently normal chromosomes. The stomata have concave lateral lobes, a feature which is unusual in *Haworthia* but which has been observed in other members of the *Aloineae* by the present authors (unpublished).

There is a distinct possibility that this is a hybrid population derived from tetraploid *H. coarctata* nearby with gene introgression from undiscovered or extinct tetraploids of the normally diploid *H. reinwardtii* growing to the east, near the Fish River.

(c) *Pentaploids*

There appears to be only one pentaploid, called *H. glauca* var. *herrei* f. *armstrongii* (von Poelln.) Bayer. It shows clear affinities with tetraploid *H. coarctata* in its leaf surface structure. It cannot be conspecific with *H. glauca* on either cytological or anatomical evidence, since *H. glauca* is hexaploid and has a most unusual leaf surface (Fig. 11d). We therefore propose reinstatement of the name *H. armstrongii* von Poelln. for this taxon.

There is controversy over whether a single clone of probably hybrid origin should be given specific rank. Here it seems reasonable since the plants are morphologically distinct and are genetically isolated from crossing with sympatric species of *Haworthia*, since they are pentaploid and totally sterile. A precedent for this decision is *H. browniana* von Poelln. which has also been shown to be a single clone occurring in one locality (Brandham and Johnson, 1977a).

(d) *Hexaploids*

The hexaploid specimens of *H. coarctata* from Rooidrift to the north of the main distribution could have arisen from the western tetraploid group by fusion of a normal and an unreduced gamete. Other hexaploid *H. coarctata* occupying habitats on high ground to the west of the Rooidrift population are probably all closely related and link with the hexaploid *H. glauca* at Locality 117. However, *H. glauca* (Figs 5g, 11d) is anatomically distinct from the other hexaploids, which have a type of stoma intermediate between those of *H. coarctata* and *H. reinwardtii*, with slightly irregular lobes.

One published record (Snoad, 1951) states that *H. glauca* is tetraploid, but since he worked mainly on cultivated material of unknown wild origin the identity of his specimen could have been in doubt.

Figure 12 summarises the inter-population affinities that we have described above and indicates the probable evolutionary trends within the group.

Ploidy level and cell size

Reference to Table 2 shows that there is not a steady increase in cell size in relation to ploidy level. Cells of triploids and tetraploids are larger than those of diploids but are similar in area to each other. Cells of pentaploids and hexaploids are still larger in area but are also similar to one another.

It has been noted that "odd number" polyploids are often disproportionately vigorous (e.g. Williams, 1964). This may well explain the results here, where triploids have cells which are as large in mean surface area as those of tetraploids, and pentaploids have cells slightly larger on average than those of hexaploids.

If we consider just the even number polyploids we find that there is a progressively larger cell surface area with increased ploidy level. Cell volumes cannot

be calculated from these data. The thickness of epidermal cells in relation to cell height and width is variable between specimens and each one would need to be measured individually if such calculations were required.

The significance and distribution of the chromosome interchanges

It has been stated above that a certain amount of morphological variation was encountered in several populations of the species studied. We could find no correlation between these variants and whether or not they were interchange heterozygotes. Thus no position effect of the alteration of the gene linkage groups associated with chromosome interchange could be detected, unlike that which was found earlier in *H. reinwardtii* f. *chalumensis* (Cutler, 1978a). However, the interchanges were found only in the heterozygous state in the diploids and as simplex heterozygotes in the tetraploids, so it must remain uncertain whether a position effect of the chromosome rearrangements would be apparent in interchange homozygotes.

The occurrence of interchanges in the *Aloineae* is of considerable interest as a source of potential karyotype alteration and evolution in this group, which is otherwise very stable in its gross chromosome morphology. Curiously, the distribution of interchange hybridity in the tribe is markedly non-random. We have examined the chromosomes of many thousands of individuals encompassing the entire tribe and have observed interchanges to occur extremely sporadically in the genera *Aloe* and *Gasteria*, which are close relatives of *Haworthia*. (Brandham 1969, 1973, 1976; Brandham and Johnson, 1977a); the incidence of interchange hybridity being in the order of 1 %.

On the other hand this study has shown that the interchange frequency is much higher in *Haworthia* section *Coarctatae* than in the rest of the tribe or even the rest of the genus, interchange hybridity having been found in 29 of the 282 plants studied here, an overall frequency of 10.3 % (Table 1). Within the *Coarctatae* this very high figure is greatly exceeded in *H. reinwardtii* f. *chalumensis*, in which of 145 individuals that were studied 113 contained interchanges, a frequency of 77.9 % (Brandham, 1974).

The reason why interchanges should be so common in the section *Coarctatae* of *Haworthia* and relatively rare in the rest of the *Aloineae* remains unknown. Within the tribe as a whole polyploidy is also largely confined to the *Coarctatae*, but any suspected correlation between polyploidy and high interchange frequency must now be discounted in view of the fact that polyploid *Aloe* species and polyploid *Haworthia* species outside the *Coarctatae* were found to have a low frequency of interchange hybridity in common with the remainder of the tribe (Brandham, 1976; Brandham and Johnson, 1977a).

The distribution of interchange hybridity is thus grossly non-random among the individual plants of the *Aloineae* sampled to date. Within the karyotype some earlier reports have indicated that the break points associated with inter-

TABLE 3.

Positions of 52 chromosome breaks involved in 26 interchanges in *Haworthia* sect. *Coarctatae*. Data from present study and from Brandham (1974); those for the short chromosomes S_1 S_2 S_3 are derived from the total short chromosome breaks divided into three equal proportions (see text).

Chromosome -no.	No. of breaks at different positions on chromosomes				Total breaks
	Short arm	Centromere	Long arm (P = proximal, D = distal)		
L ₁	2	3	1P,	2D	8
L ₂	1	0	3P,	5D	9
L ₃	0	3	3P,	4D	10
L ₄	2	1	4P,	3D	10
S ₁	0,66	2,33		2	5
S ₂	0,66	2,33		2	5
S ₃	0,66	2,33		2	5

change are also non-randomly distributed within and between the individual chromosomes. For instance, Riley and Majumdar (1968) summarised their previous work on interchanges in *Haworthia*, surveying six straightforward exchanges and one other in which breaks had occurred in three chromosomes. They found that the positions of the break points in the chromosomes involved in the exchanges were not randomly distributed. Of their total of 15 breaks no fewer than 13 were at the centromeres and only two were elsewhere. Furthermore, the L_1 chromosome was involved in six of the seven interchanges; and this too is clearly not a random occurrence.

Observations on 12 interchanges in *H. reinwardtii* f. *chalumnensis* by Brandham (1974) were added to those of Riley and Majumdar and tended to confirm this non-random distribution of break points, but when the f. *chalumnensis* results are added to the 14 interchanges described in the present study (those of Riley and Majumdar being excluded) a different picture emerges. In these two studies the 26 interchanges which have been analysed and illustrated provide a total of 52 chromosome breaks, which is a sample large enough to form the basis for a more meaningful survey of break point distribution, restricted as it is to only two very closely related species within the genus.

The positions of these breaks are given in Table 3. In this table the total of 15 short chromosome breaks has been arbitrarily divided among the three short chromosome sets, the S_1 , S_2 and S_3 . This was necessary because it will be recalled that no attempt was made to separate these extremely similar chromosomes into three sets of homologues. The table shows that in this sample of interchanges the breaks are largely random in distribution, a finding which is contrary to that of Riley and Majumdar (1968). There is no tendency for the L_1 to be involved any more frequently than the other long chromosomes. In fact it is apparent that breaks occur in all four long sets with approximately equal fre-

quency. There is, however, a slight tendency for more breaks to occur in the short chromosomes than would be expected on the assumption that break frequency is proportional to chromosome length. The frequency in the short chromosomes can be seen from Table 3 to be half that in the long chromosomes, whereas the illustrations in this article (e.g. Fig. 4) show that the actual length of the short chromosomes is very much less than half that of the long ones.

Within chromosomes the break points are also distributed almost at random with only a very slight tendency towards preferential breakage through the centromere, which is a recognised "weak point" (Brandham, 1974). Assuming complete randomness, the frequency of breaks through the centromere should drop almost to zero. Table 3 shows that although the frequency of such breaks is lower than that found by Riley and Majumdar (1968) they are nonetheless a significant proportion of the total number of breaks.

Several of the interchanges in *Haworthia* are of the centric fusion type, with breaks through or near the centromeres of two acrocentrics followed by reunion to give a large metacentric derived from the long arms and a short metacentric or submetacentric from the short arms. Examples are interchange A, B and E in *H. reinwardtii* f. *chalumensis* (Brandham, 1974), and 3, 5 and 7 in this study.

This type of chromosome interchange is well known under the term Robertsonian fusion, and in many organisms the shorter interchange chromosome is lost following such an event, the interpretation of which is that the organism can tolerate the loss of the genes situated on the short arms (if any). With the establishment of homozygosity for this type of Robertsonian fusion there is a net loss of two chromosomes from the complement (in fact only two centromeres and two pairs of short arms are lost) and a new stable karyotype is established (Jones, 1974). In all records of Robertsonian fusion in the *Aloineae* published to date by Riley and his co-workers and by ourselves (Brandham, 1973, 1974, 1976; Brandham and Johnson, 1977a) the short interchange chromosome is never lost and there is no net lowering of the chromosome number. It is thus apparent that the short arms of the acrocentric chromosomes of *Haworthia* and probably of the rest of the *Aloineae* possess genes without which the plants cannot survive.

One problem remains to which no satisfactory answer can yet be put forward. Although interchanges are by now known to occur throughout the *Aloineae* and are even relatively common in the section *Coarctatae* of *Haworthia* no instance has yet been found of a naturally-occurring homozygote. As a result of a Robertsonian interchange involving non-homologous long acrocentric chromosomes in which the arms are rearranged following breakage to produce a very long metacentric and a short metacentric, a diploid homozygote would have one pair of very long metacentrics, two pairs of normal long acrocentrics, one pair of short metacentrics and three pairs of normal short acrocentrics. Such a homozygote would be expected to have regular meiosis, forming seven biva-

lents, and it would be fully fertile. The karyotype would then constitute a major departure from the standard *Aloineae* karyotype and would form the foundation of further evolutionary departures since it would be to some extent isolated genetically from the non-interchange homozygotes.

The reason why these homozygotes have not occurred, or if they do occur, the reason why they do not persist is not known. Certainly interchange heterozygotes in the *Aloineae* are capable of reproducing sexually in the wild, as has been shown earlier, both in *Aloe* (Brandham and Johnson, 1977a), and in *Haworthia reinwardtii* f. *chalumensis* (Brandham, 1974). This observation is confirmed by the present study, which has demonstrated that sexually-produced rearrangements of different interchanges occur at Locality 91. Those involved are interchange 1A or one of its altered chromosomes ("Deletion 2"), which are found either alone or associated with interchanges 3 or 4 in different plants (Table 1).

It is therefore theoretically possible for interchange homozygotes to occur in the wild in the seed progeny of heterozygotes in the second or further generations following the initial mutation (allowing for the fact that most *Aloineae* are self-incompatible), but it is evident that since they have not been found they must be selected against if formed. The basic karyotype of four long and three short acrocentric chromosomes in the *Aloineae* is therefore maintained.

White (1963) introduced the term "karyotype orthoselection" as a mechanism by which the basic karyotype of a taxon or series of related taxa remains unchanged despite the sporadic occurrence of various chromosomal changes in the heterozygous condition. It was considered that the particular karyotype typical of the taxon is the optimal one. All deviant karyotypes are thus subjected to adverse selection pressures and are eliminated. Even though structural chromosome changes are now known to occur at quite high frequencies in *Haworthia* section *Coarctatae*, and at lower but still significant frequencies in the rest of the *Aloineae* they have yet to be found as homozygotes. The stable bimodal karyotype which is found in every one of the hundreds of species comprising the *Aloineae* tribe may therefore be considered as one of the strongest known examples of karyotype orthoselection.

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WILLIAM FREDERICK PURCELL AND THE FLORA OF BERGVLIET

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(*Compton Herbarium, Kirstenbosch*)

ABSTRACT

W. F. Purcell's herbarium of vascular plants from Bergvliet, Cape Peninsula, is enumerated, the specimens having recently been named and incorporated in the South African Museum Herbarium, Kirstenbosch. Formed between 1915 and 1919 from a low-land/flats site, now destroyed by urbanisation, the 2 513 sheet collection records the presence of 595 indigenous species, i.e. 26,4 % of the Cape Peninsula's flora from 0,7 % of its surface area. A brief biography of Purcell is provided.

UITTREKSEL

WILLIAM FREDERICK PURCELL EN DIE FLORA VAN BERGVLIET

W. F. Purcell se herbarium van vaarplante vanaf Bergvliet in die Kaapse Skiereiland word genoem nadat die soorte pas benaam en opgeneem is in die Suid-Afrikaanse Museum-herbarium versameling, Kirstenbosch. Saamgestel tussen 1915 en 1919 van 'n laagland/vlakte terrein, nou verlore as gevolg van dorpsuitbreiding, verteenwoordig die 2 513 eksemplare die teenwoordigheid van 595 soorte wat 26,4 % van die Skiereilandse flora uitmaak uit 'n area 0,7 % van die totale oppervlakte. 'n Kort biografie van Purcell word voorsien.

INTRODUCTION

During 1977/78, 2 513 mounted herbarium specimens, collected approximately eighty years ago by Dr W. F. Purcell at Bergvliet Farm, Constantia, near Cape Town, were identified, accessioned and incorporated into the general collection of the South African Museum Herbarium at Kirstenbosch. This material documents the former floristic richness of what is today a densely populated part of the Cape Peninsula.

Since the Purcell collection is relatively unknown, we have deemed it desirable to chronicle the history of this material, to provide a brief biography of the collector, a list of the taxa represented in the Bergvliet collection and also a discussion on the collection's significance in making analyses of the Cape Peninsula's flora.

HISTORY OF THE COLLECTION

In 1921, Mrs Anna Purcell, widow of Dr W. F. Purcell, donated her late husband's herbarium to the South African Museum, Cape Town. According to the annual report of the museum for 1921, the herbarium consisted of an

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"admirably mounted set of native plants representing the flora of the Bergvliet estate. The specimens, which have been most carefully dried, are, in most instances, mounted and kept separate from the general collection, occupying four cabinets." (Ann. Rep. of S.A. Museum, 1921 pg. 10).

Unfortunately, the specimens were mostly unidentified. Consequently they remained as a separate collection and were neither loaned to, nor examined by research workers, with the exception of Sydney Garside who studied the Hypoxidaceae sheets. Garside excepted, none of the other contributors to Adamson and Salter's *Flora of the Cape Peninsula* (1950) apparently made any use of this material—a fact which resulted in at least two species' records for the Cape Peninsula being overlooked. (Records of *Galaxia alata* Goldblatt and *Moraea inconspicua* Goldblatt from the Cape Peninsula, are each based on a Purcell specimen and one other collection).

In 1956, the South African Museum Herbarium was transferred to Kirstenbosch and with it came the Purcell collection, still unworked and still in its four original cabinets. As a detailed inventory of the flora peculiar to a lowland/flats site on the Cape Peninsula, it was obvious that Purcell's herbarium constituted the finest existing record.

Accordingly, the present authors (with the assistance of several specialists) undertook the identification of the material and incorporated it in the South African Museum Herbarium. A distinctive ticket was affixed to each sheet indicating its provenance and also providing further data such as the specimen's precise locality on the Bergvliet estate, the date or dates of collection and where known, Purcell's collecting number.

THE SPECIMENS

A remarkable feature of Purcell's herbarium specimens is their completeness and quality of preservation. Root systems were carefully excavated, washed clean and pressed. Fugacious flowers (e.g. Iridaceae) were carefully laid out and populations were sampled to display size ranges within a species. Moreover, it is clear from their exceptionally fine state of preservation that the specimens were killed rapidly, followed by swift dehydration during the drying process. Purcell was especially successful with fleshy material and indeed left a number of manuscript notes on his experiments in drying botanical specimens.

Practically all his botanical collections at Bergvliet were made during a four year period, between 1915 and his death in 1919. Not all these collections bear personal collecting numbers. Collecting numbers up to 525 have been encountered, although his Bergvliet register enumerates collections from 1 to 361, after which he apparently discontinued writing up the register. This register is now preserved in the Compton Herbarium, Kirstenbosch.



FIG. 1.
William Frederick Purcell

OTHER COLLECTING LOCALITIES

Although practically all Purcell's collecting was confined to Bergvliet Farm, a few hundred sheets from other localities were also incorporated into the general SAM herbarium. This additional material was collected chiefly at The Baths, Caledon, and near Riviera Beach, Hermanus, as well as at a few sites on the Cape Peninsula, such as Hout Bay, but is not further discussed here.

BRIEF BIOGRAPHY

William Frederick Purcell was born in London on the 18th of September 1866. His father, Walter Patrick Joseph Purcell of Waterford, Ireland, had married Sophia Wilhelmina Jonasina Hertzog in Cape Town, during November 1865. Before coming to the Cape, W. P. J. Purcell had originally taken a medical degree and practised as a naval surgeon, although later he decided to pursue a legal career. He was admitted as a barrister of the Inner Temple, London, and in due course joined the Cape Bar, but it is not certain whether he ever practised.

Young William Frederick was brought up in an atmosphere of the best Cape traditions. Through his mother (who was a second cousin to Gen. J. B. M. Hertzog) he was connected to some of the most influential families in the land. Much of his childhood was spent at Bergvliet, the historic home owned by his uncle, W. F. Hertzog. Three aspects of life at Bergvliet were to influence him profoundly. The wild life on the farm led him to take up a career in zoology, while the largely unspoilt natural vegetation was to be a source of boundless interest and pleasure in his retirement.

The old homestead with its library, the collection of furniture inherited from his mother and his friendship with Mrs Marie Koopmans de Wet, stimulated a life-long preoccupation with art and antiques, that culminated in his successful efforts to establish a cultural museum in Mrs Koopmans de Wet's house. (He was one of the executors of Mrs Koopmans de Wet's will).

Purcell's cultural and zoological activities are well documented but his work as a plant collector is scarcely known. This paper attempts to put on record his achievements in this field.

Purcell's scientific career began in 1881 when he entered the South African College, Cape Town. After graduating in 1887, as a Bachelor of Arts (in Mathematics and Natural Philosophy), he proceeded to the Friederick Wilhelm University, Berlin, where he obtained the degree of Doctor of Philosophy in August 1896, his thesis being on 'The structure of the eyes in the *Phalangida*.'

On returning to the Cape, Purcell joined the South African Museum as first assistant in the Department of Invertebrates. He held this post from 1896 until July 1905, when he resigned due to ill health. Retiring to Bergvliet, he spent the remaining years of his life there, collecting Arachnids and making an herbarium

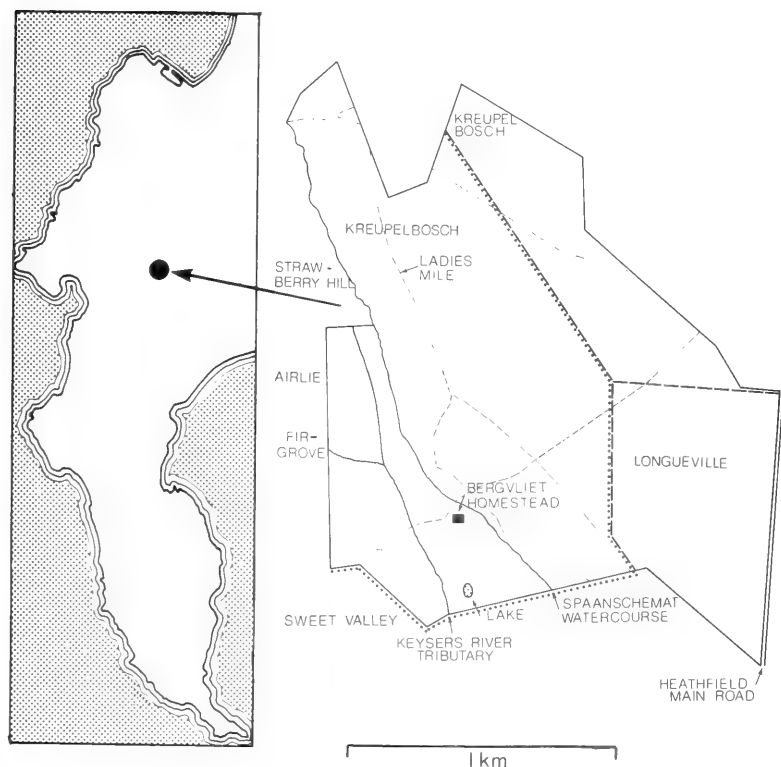


FIG. 2.

Bergvliet estate, showing the perimeter boundaries of the property and its position on the Cape Peninsula.

of the farm's flora. Never a robust man, Purcell had to nurse a delicate constitution. He died at Bergvliet on the 3rd of October 1919, at the early age of 53.

BRIEF HISTORY OF THE ESTATE

To understand the history of Bergvliet and the flora this estate supported, it is necessary to look back to the year 1685, when Governor Simon van der Stel was granted a farm and grazing rights in an area south-west of Table Mountain; a farm which he subsequently called Constantia. Van der Stel died in 1712 but four years later, in August 1716, the executors of his estate divided the property into two portions, Constantia and Bergvliet. Thus Bergvliet came into existence



FIG. 3A.



FIG. 3B.

Typical examples of Purcell's herbarium specimens showing the careful manner of preparation.

as a separate entity, although it was originally part of Van der Stel's farm on which he had exercised grazing rights only. Consequently, it was not subject to any agricultural development during this period.

Between 1716 and 1769 several different persons held title to Bergvliet, but in 1769 Petrus Michel Eksteen acquired the farm and it was he who, in 1775, erected the handsome residence which is still standing today. Three generations of the Eksteen family farmed Bergvliet, until it was again sold, this time passing into the possession of William Frederick Hertzog, in 1865. On Hertzog's death in 1902, Bergvliet passed to his two sisters, Mrs S. W. J. Purcell and Mrs A. M. Jeffcoat. Dr W. F. Purcell, son of Mrs S. W. J. Purcell, managed the farm on behalf of his mother and aunt, between 1902 and 1919, the period during which he began to survey the flora of Bergvliet.

With the death of Dr W. F. Purcell in 1919, the Rev W. Jeffcoat assumed stewardship of the farm on behalf of the family. This situation continued until about 1930, when the farm was divided, the Jeffcoat's acquiring Bergvliet and the upper or northern portion, Kreupelbosch, going to the Purcell descendants. This latter event marks the end of the rural phase in Bergvliet's history. Sub-urban development was already fast encroaching.

In April 1945, the Divisional Council of the Cape purchased Bergvliet from the Rev W. Jeffcoat for a paltry £15,000 to provide (as had been Jeffcoat's wish and intention), a housing estate for ex-servicemen. In 1952, the upper part of Kreupelbosch, now called Meadowridge, fell to the developers. Today Bergvliet, as it was known to Dr W. F. Purcell, is merely a suburb of greater Cape Town.

From the time of the original land grant until the death of Dr W. F. Purcell in 1919, the natural vegetation cover at Bergvliet appears to have suffered surprisingly little damage. The agricultural development that did take place was largely confined to the fertile valley through which the Keyser's river flows. To the north and east of the homestead lay an area of comparatively undisturbed veld. This veld was used for grazing but due to the rather sandy soil conditions, it was never ploughed. Such was the situation when Purcell started his collecting programme, although invasive pest plants, chiefly *Acacia saligna* and *Pinus pinaster*, were beginning to become a problem.

Purcell must have been very conscious of the destruction being wrought by advancing suburbia. He must also have been perturbed by the effect of grazing on the veld, for he arranged for extensive portions of the farm to be encamped so as to prevent the entry of grazing animals while his survey was in progress. It was therefore with a certain sense of urgency that he devoted the last years of his life to surveying the farm's flora, amassing an herbarium of over 2 500 sheets during that period. Just how comprehensive Purcell's records of the flora of Bergvliet were at the time of his death, we will never know, but they must have been fairly complete.

THE FLORA

Most lowland areas of the Cape Peninsula are now covered by urban sprawl and consequently little, if any, of the natural vegetation there has survived. The Bergvliet check-list is thus of particular importance as it is the only reasonably complete floristic list for a lowlands/flats habitat on the Cape Peninsula.

Situated at a mean elevation of 15 metres above sea level, the surface geology of Bergvliet is dominated by Tertiary to Recent sands in the south, while along the north-western boundary, the soils are derived from pre-Cape Granite. While Purcell was conducting his collecting programme, the estate was made up of several farms, Bergvliet itself, Kreupelbosch and Longueville (Fig. 2), the whole amounting to approximately 343 hectares (\pm 400 morgen). From this area 595 species of indigenous vascular plants were recorded: 1 pteridophyte, 1 gymnosperm, 185 monocotyledons and 408 dicotyledons. (74 naturalised aliens were also recorded.)

TABLE 1
Species densities from different areas on the Cape Peninsula.

Locality	Cape Peninsula	Cape of Good Hope Nature Reserve	Kirstenbosch Estate	Bergvliet Farm
Surface area in square kilometres	471	77	5,28	3,43
Total number of indigenous vascular plant species (Pteridophytes, Gymnosperms, Angiosperms) excluding naturalised aliens	2 256	1 035	920	595
Percentage of the Cape Peninsula's Flora	100 %	45,8 %	40,7 %	26,4 %

Thus the Bergvliet estate supported 26.4 % of the indigenous species of vascular flora recorded from the Cape Peninsula on a mere 0,7 % of the Peninsula's total surface area! Such figures again emphasise the exceptionally high species' densities in relatively small areas, which have been recorded for the Cape Peninsula (Table 1).

The Cape of Good Hope Nature Reserve (Taylor, 1969) and Kirstenbosch estate (Anon, 1978) are the only other intensively surveyed local areas on the Cape Peninsula, for which floristic data are available. (Tables 1 and 2.) Unlike Bergvliet, these are largely upland or mountainous areas, where soils are almost entirely derived from Table Mountain Sandstone and where shrubby or perennial genera dominate the lists of the largest genera recorded there.

TABLE 2

Comparison between the Kirstenbosch Estate, Cape of Good Hope Nature Reserve and Bergvliet Estate, showing the largest genera, in order of importance, recorded from these areas; species' numbers are given in brackets.

Kirstenbosch Estate (National Botanic Gardens preliminary check-lists, 1978)	Cape of Good Hope Nature Reserve (Taylor, 1969)	Bergvliet Estate
<i>Erica</i> (43)	<i>Erica</i> (22)	<i>Oxalis</i> (18)
<i>Senecio</i> (22)	<i>Ficinia</i> (17)	<i>Erica</i> (14)
<i>Helichrysum</i> (21)	<i>Aspalathus</i> (16)	<i>Senecio</i> (14)
<i>Tetraria</i> (17)	<i>Tetraria</i> (15)	<i>Moraea</i> (13)
<i>Ficinia</i> (15)	<i>Restio</i> (13)	<i>Crassula</i> (12)
<i>Oxalis</i> (14)	<i>Cliffortia</i> (11)	<i>Gladiolus</i> (11)
<i>Aspalathus</i> (14)	<i>Pentaschistis</i> (10)	<i>Helichrysum</i> (11)
<i>Cliffortia</i> (13)	<i>Thesium</i> (9)	<i>Pelargonium</i> (10)
<i>Crassula</i> (13)	<i>Helichrysum</i> (8)	<i>Psoralea</i> (9)
<i>Restio</i> (12)	<i>Psoralea</i> (7)	<i>Cliffortia</i> (8)
	<i>Crassula</i> (7)	<i>Ficinia</i> (8)
	<i>Elegia</i> (7)	

In contrast, geophytes such as *Oxalis* (18 species), *Moraea* (13 species), *Gladiolus* (11 species), as well as certain tuberous *Pelargonium* species, are important among the largest genera at Bergvliet. While there are certain similarities between the three lists, it seems that edaphic conditions and also the lowland/flats habitat at Bergvliet, have favoured the establishment of geophytic life forms. Clearly, the loss of this specialised habitat has resulted in a substantial impoverishment of the Cape Peninsula's flora.

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The authors are much indebted to Mrs J. M. H. Purcell of Kreupelbosch, Meadowridge, for providing biographical data on Dr W. F. Purcell (her late father-in-law) and for many other personal reminiscences. We also wish to thank the following specialists for assisting in identifying the herbarium specimens: Prof E. A. Schelpe, Dr A. V. Hall and Mr P. Linder (Orchidaceae), Dr P. Goldblatt (Iridaceae), Prof M. P. de Vos (*Romulea*), Dr H. Tolken (Crassulaceae), Mrs M. Rand (Hypoxidaceae), Miss E. Esterhuysen (Restionaceae), Mrs A. A. Mauve-Obermeyer (*Tenicroa* and *Urginea*), Dr Ion Williams (*Leucadendron*) and Dr Peter Raven (*Oenothera*).

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CHECK LIST OF THE FLORA OF BERGVLIET ESTATE

Aliens are marked with an asterisk*. Numbers placed after each name are the sheet registration in the South African Museum Herbarium. Families, genera and species arranged according to Adamson & Salter (1950).

6. SCHIZAEACEAE

Schizaea pectinata (L.) Swartz 91059.

13. PINACEAE

**Pinus pinea* L. 91030.

14. CUPRESSACEAE

Widdringtonia nodiflora (L.) Powrie 91031.

15. TYPHACEAE

Typha latifolia L. ssp. *capensis* Rohrb.
91020–91026; 91028; 91029.

18. SCHEUCHZERIAEAE

Triglochin striata Ruiz. & Pav. 91039;
91040.
bulbosa L. 91041–91058.

20. GRAMINEAE

Cymbopogon marginatus Stapf. 91038.
Ehrharta bulbosa Sm. 91032.
Stipagrostis zeyheri (Nees) de Wint. 91037.
Pentaschistis sp. 91036.
Eragrostis capensis (Thunb.) Trin. 91033–
91035.

21. CYPERACEAE

Cyperus ? *rotundus* L. 90929; 90930.
Scirpus antarcticus L. 90922.
hystrix Thunb. 90921.
Ficinia deusta (Berg.) Levyns 90912–
90917.
tristachya (Rottb.) Nees 90909–90911.
paradoxa (Schrad.) Nees 90908.
indica (Lam.) Pfeiff. 90905; 90906.
bulbosa (L.) Nees 90901–90904.
secunda (Vahl) Kunth 90907.

Ficinia pallens (Schrad.) Nees 90918; 90919.
radiata Kunth 90900.

Fuirena hirsuta (Berg.) P. L. Forbes 90920.
Asterochaete glomerata (Thunb.) Nees
90931.

Tetralia cuspidata (Rottb.) C.B. Cl. 90924
–90927.

compar (L.) Lestib. 90923.

bromoides (Lam.) Pfeiff. 90928.

Carex aethiopica Schkuhr. 90932

22. ARACEAE

Zantedeschia aethiopica (L.) Spreng.
91060

24. RESTIONACEAE

Restio tetragonus Thunb. 90845.
harveyi Mast. 90846.
Chondropetalum microcarpum (Kunth)
Pillans 90836–90839.
Thamnochortus fruticosus Berg. 90843;
90844.
Willdenowia striata Thunb. 90840–90842.

29. LILIACEAE

Tulbaghia alliacea L.f. 91121; 91123–
91126.
Kniphofia uvaria (L.) Hook f. 90933;
90934.
Asparagus capensis L. 90889.
asparagoides (L.) Wight 90879–90885.
crispus Lam. 90886–90888.
rubicundus Berg. 90894–90897.
Eriospermum nanum Marloth 90984–
90987.
lanceaeifolium Jacq. 90988–90992; 90996;
90997; 90999–91001.
cernuum Baker 90993–90995; 90998 sp.
91002–91006.

- Trachyandra filiformis* (Ait.) Oberm. 90967–90969.
chlamydophylla (Bak.) Oberm. 90954–90956.
hispida (L.) Kunth 90938–90944.
hirsutiflora (Adamson) Oberm. 90949–90953.
ciliata (L.f.) Kunth 90935–90937.
hirsuta (Thunb.) Kunth 90963–90966.
brachypoda (Bak.) Oberm. 90957–90962.
Anthericum rangei Engler & Krause 90945–90948.
Caesia contorta (L.f.) Dur. & Schinz 91122; 91127–91131.
Bulbine favosa Roem. & Schult. 90971–90977.
lagopus (Thunb.) N.E. Br. 90978.
pugioniformis Link 90979–90983.
Bulbinella triquetra Kunth 90970.
Ornithogalum hispidum Hornem. ssp. *bergii* (Schtld.) Oberm. 91115–91120.
graminifolium Thunb. 91110–91112; 91114.
dregeanum Kunth 91113.
Albuca canadensis (L.) Leighton 91088–91091.
cooperi Baker 91093.
juncifolia Baker 91092.
Tenicroa filifolia (Jacq.) Oberm. 91098; 91105–91109.
young filifolia (Jacq.) Oberm. 91099.
exuviata (Jacq.) Speta. 91100–91104.
Urginea ecklonii Baker 91096.
? ecklonii Baker 9194; 91095; 91097.
Lachenalia rubida Jacq. 90383; 90386.
unifolia Jacq. var. *wrightii* (Bak.) Bak. 90379; 90380.
variegata Barker 90381; 90382; 90387.
orchoides (L.) Ait. 90388–90390.
reflexa Thunb. 90384; 90385.
Baometra uniflora (Jacq.) Lewis 91068; 91069.
Dipidax punctata (L.) Hutch. 91075–91079.
Wurmbea spicata (Burm.) Dur. & Schinz 91070–91072.
Ornithoglossum viride (L.f.) Ait. 91073; 91074.
Androcymbium capense (L.) Krause 91080–91084.
eucomoides (Jacq.) Willd. 91085–91087.
30. HAEMODORACEAE
Wachendorfia thyrsoflora L. 90847.
- Wachendorfia paniculata* L. 90848; 90849; 90857–90861.
brachyandra Barker 90850–90853.
parviflora Barker 90854–90856.
31. AMARYLLIDACEAE
Haemanthus rotundifolius Ker-Gawl. 90868–90872.
Boophane guttata (L.) Herb. 90873–90875.
Brunsvigia orientalis (L.) Ait. ex Eckl. 90876–90878.
Gethyllis pusilla Baker 91010; 91011.
afra L. 91007–91009; 91012–91019.
Hessee cinnamomea (L'Hérit.) Dur. & Schinz 90864–90867.
Pauridia minuta (L.f.) Dur. & Schinz 90862; 90863.
Empodium plicatum (Thunb.) Garside 91061–91067.
Spiloxene alba (Thunb.) Fourc. 91285–91287.
schlechteri (H. Bol.) Garside 91237–91245.
curculigoides (H. Bol.) Garside 91279–91284.
capensis (L.) Garside 91223–91236; 91248–91278.
canaliculata Garside 52052; 91247.
gracilipes (Schltr.) Garside 91246.
32. IRIDACEAE
Romulea flava (Lam.) De Vos var. *flava* 91136–91142; 91154.
flava (Lam.) De Vos var. *minor* (Beg.) De Vos 91132–91135.
flava (Lam.) De Vos var. *viridiflora* (Beg.) De Vos 91143–91150.
hirsuta Bak. 91176; 91177.
triflora (Burm.) N.E. Br. 91178–91181.
cruciata Bak. var. *intermedia* (Beg.) De Vos 91166.
rosea (L.) Eckl. var. *australis* (Ewart) De Vos 91167; 91182–91189; 91194–91196.
rosea (L.) Eckl. var. *communis* De Vos 91168–91172; 91190–91193.
rosea (L.) Eckl. var. *reflexa* (Eckl.) Beg. 9115–91165.
rosea (L.) Eckl. var. *rosea* 91173–91175.
obscura Klatt 91151–91153.
Galaxia alata Goldblatt 93388.
versicolor Salisb. ex Klatt 93389.
Hexaglottis virgata Sweet 90137; 90138.
lewisiae Goldbl. 90135; 90136.

- Moraea angusta* (Thunb.) Ker 59718.
bituminosa (L.f.) Ker 90230–90232.
gawleri Spreng. 90172; 90233; 90174; 90176; 90177.
elsiae Goldbl. 90173; 90175.
fugax (de la Roche) Jacq. 90133; 90190; 90192–90194; 90134.
inconspicua Goldbl. 90062–90064.
lugubris (Salisb.) Goldbl. 90222; 90224; 90227.
neglecta Lewis 59719.
papilionacea (L.f.) Ker 90223; 90225; 90226; 90228; 90229.
ramosissima (L.f.) Druce 90184–90186.
tricuspidata (L.f.) Lewis 90178–90181.
tripetala (L.f.) Ker 90187–90189; 90191.
vegeta L. 90182; 90183.
Homeria collina Vent. 93362–93376; 93400; 93401.
flaccida Sweet 93349–93356; 93393–93396; 93402.
miniata (Andr.) Sweet 93377–93380.
minor (Eckl.) Goldbl. 93357–93361; 93392; 93397–93399.
Aristea spiralis (L.f.) Ker 90119.
macrocarpa Lewis 90117; 90118.
pauciflora W. Dod 90120–90122.
cuspidata Schinz 90126–90128.
africana (L.) Hoffmssg. 90123–90125.
glauca Klatt 90114–90116.
Watsonia pyramidata (Andr.) Stapf 90202; 90203.
angusta Ker 90204.
meriana Mill. 90129.
humilis Mill. 90130–90132.
Micranthus alopecuroides (L.) Eckl. 90104–90113.
tubulosus (Burm.) N.E. Br. 90095–90100.
junceus (Bak.) N.E. Br. 90101–90103.
Thereianthus bracteolatus (Lam.) Lewis 90201.
Lapeirousia corymbosa (L.) Ker ssp. *corymbosa* 90197–90200.
anceps (L.f.) Ker 90195; 90196.
Antholyza ringens L. 90208–90210.
Babiana stricta (Ait.) Ker var. *stricta* 90072; 90073.
villosula (Gmel.) Ker ex Steud. 90080; 90083; 90085; 90074–90076.
ambigua (R. & S.) Lewis 90078; 90079; 90081; 90082; 90084; 90086.
Sparaxis grandiflora (de la Roche) Ker 90087–90091.
bulbifera (L.) Ker 9002.
Anapalina triticea (Burm.) N.E. Br. 90212–90214.
Tritoniopsis parviflora (Jacq.) Lewis 90205.
Ixia polystachya L. 90215–90221.
Hesperantha pilosa (L.f.) Ker 93334; 93335.
graminifolia D. Don 93331–93333.
falcata (L.f.) Ker 93336.
Engysiphon roseus (Schinz) Lewis 90093; 90094.
Geissorhiza aspera Goldblatt 9326–93330; 93337–93339.
ovata (Burm.) Asch & Graeb. 93346–93348.
junceus (Link) A. Dietr. 93344; 93345.
humilis Ker 93342; 93343; 93390; 93391.
imbricata (de la Roche) Ker 93340; 93341.
Gladiolus alatus L. var. *alatus* 90149; 90150.
punctulatus Schrank var. *punctulatus* 90155–90157.
brevifolius Jacq. 90069; 90139–90144.
ornatus Klatt 90066; 90067.
carneus de la Roche 90158.
undulatus L. 90163; 90164.
carinatus Ait. 90170; 90171.
gracilis Jacq. 90065; 90159–90162; 90165–90169.
maculatus Sweet 90151–90154.
hyalinus Jacq. 90145–90148.
liliceus Houtt. 90068; 90070; 90071.
Homoglossum priori N.E. Br. 90211.
Chasmanthe aethiopica (L.) N.E. Br. 90206; 90207.

33. ORCHIDACEAE

- Acrolophia bolusii* Rolfe 91210.
lamellata (Lindl.) Schltr. & Bol. 91211; 91221.
Eulophia aculeata (L.f.) Spreng ssp. *aculeata* 91209.
Holothrix villosa Lindl. 91201; 91202.
Satyrium ligulatum Lindl. 91208.
bicorne (L.) Thunb. 91203.
coriifolium Swartz 91206.
odorum Sond. 91205; 91222.
bicallosum Thunb. 91207.
bracteatum (L.f.) Thunb. 91204.
Monadenia atrorubens (Schltr.) Rolfe 91218.
bracteata (Sw.) Dur. & Sch. 91219; 91220.
Herschelia lacera (Swartz) Lewis 91216; 91217.

- Disa cornuta* (L.) Swartz 91215.
Disperis capensis (L.f.) Swartz 91199.
villosa (L.f.) Swartz 91197; 91198.
Ceratandra atrata (L.) Dur. & Schinz
 91200.
Corycium orobanchoides (L.f.) Swartz
 91212.
Pterygodium catholicum (L.) Swartz 91213;
 91214.

35. SALICACEAE

- Salix hirsuta* Thunb. 90835.

36. MYRICACEAE

- Myrica quercifolia* L. 90832; 90833.
serrata Lam. 90834.

41. URTICACEAE

- **Urtica urens* L. 90831.

42. PROTEACEAE

- Leucadendron floridum* R. Br. 89724;
 89725; 89730.
salignum Berg. 89731–89734.
levisanus Berg. 89728; 89729.
laureolum (Lam.) Fourcade 89723.
Protea coronata Lam. 89708; 89709.
cynaroides (L.) L. 89715; 89716.
repens (L.) L. 89710–89712.
scolymocephala (L.) Reich. 89713.
acaulos (L.) Reich. 89714.
Leucospermum hypophyllocarpodendron
 (L.) Druce 89705–89707.
Diastella proteoides (L.) Druce 89726;
 89727.
Serruria fasciflora Salisb. ex Knight 89718;
 89719.
glomerata (L.) R. Br. 89717.
cyanoides R. Br. 89720.
 **Hakea tenuifolia* (Salisb.) Domin 89721.
 **gibbosa* (Sm.) Cav. 89722.

43. SANTALACEAE

- Thesium virgatum* Lam. 90771–90774.
euphrasioides A. DC. 90761.
ecklonianum Sond. 90760.
scabrum L. 90764; 90765.
capitatum L. 90766.
funale L. 90767–90770.
aggregatum A. W. Hill 90762; 90763.

45. LORANTHACEAE

- Viscum capense* Thunb. 90819; 90820.

48. POLYGONACEAE

- **Polygonum aviculare* L. 89739–89741.
salicifolium Brouss. ex Willd. 89735;
 89736.
setulosum Rich. 89778–89780.
lapathifolium L. 89737; 89738; 89742.
Rumex cordatus Desf. 89762; 89763.
sagittatus Thunb. 89761.
latalvalvis Meisn. 89747–89750.
 **crispus* L. 89755; 89757; 89758.
 **conglomeratus* Murr. 89759; 89760.
 **pulcher* L. 89753; 89754; 89756.
 **Acetosella vulgaris* (Koch) Fourr. 89743–
 89746.
Emex australis Steinh. 89764.

49. CHENOPODIACEAE

- **Chenopodium album* L. 89771–89773.
 **murale* L. 89774–89777.
Exomis microphylla (Thunb.) Aellen var.
axyroides Aellen 89765–89767.

50. AMARANTHACEAE

- **Amaranthus hybridus* L. 89800–89802.
thunbergii Moq. 89769; 89770.

52. AIZOACEAE

- Pharnaceum elongatum* (DC.) Adamson
 89876–89878.
lanatum Bartl. 89879; 89880.
dichotomum L.f. 89881.
Aizoon paniculatum L. 89866; 89867.
sarmentosum L.f. 89864; 89865.
Adenogramma glomerata (L.f.) Druce
 89870–89872.
Polpoda capensis Presl 89873–89875.
Carpanthea pomeridiana (L.) N.E.Br.
 90407.
Dorotheanthus bellidiformis (Burm.)
 N.E.Br. 90406.
Lampranthus reptans (Ait.) N.E.Br.
 90394–90396.
 ? *calcaratus* (Wolley-Dod) N.E.Br.
 90401.
emarginatus (L.) N.E.Br. 90402.
aduncus (Haw.) N.E. Br. 90400.
filicaulis (Haw.) N.E. Br. 90397–90399.
glaucus (L.) N.E. Br. 90403.
aurantiacus (DC.) Schwant. 90404;
 90405.
Ruschia sarmentosa (Haw.) Schwant.
 90393.

54. CARYOPHYLLACEAE

- **Stellaria media* (L.) Vill. 89476.
 **Spergula arvensis* L. 89475.
 **Polycarpon tetraphyllum* L.f. 89474.
Corrigiola litoralis L. 89781.
 **Silene gallica* L. 89478; 89480.
 clandestina Jacq. 89479.
 ? *burchellii* Oth. ex DC. 89481.
Dianthus albens Ait. 89482–89486.
 **Agrostemma githago* L. 89477.

55. NYMPHAEACEAE

- Nymphaea capensis* Thunb. 89466.

56. RANUNCULACEAE

- Knowltonia vesicatoria* (L.f.) Sims 89470.
Ranunculus multifidus Forsk. 89471;
 89472.

57. MENISPERMACEAE

- Antizoma capensis* (Thunb.) Diels 89467–
 89469.

58. LAURACEAE

- Cassytha ciliolata* Nees 89768.

59. PAPAVERACEAE

- **Fumaria officinalis* L. 89464; 89465.

60. CRUCIFERAE

- **Diploaxis muralis* (L.) DC. 89446; 89447.
 **Raphanus raphanistrum* L. 89440–89442.
Heliophila pusilla L.f. 89458; 89459.
 ? *coronopifolia* L. 89460.
 diffusa (Thunb.) DC. 89462.
 africana (L.) Marais 89450–89457.
 ? *pendula* Willd. 89461.
 **Coronopus didymus* (L.) Sm. 89443.
 **Capsella bursa-pastoris* (L.) Medic.
 89444; 89445.
 **Barbarea verna* (Mill.) Aschers 89448.
 **Rorippa nasturtium-aquaticum* (L.)
 Hayek 89463.

62. DROSERACEAE

- Drosera cistiflora* L. 89836–89840.
trinervia Spreng. 89844; 89845.
capensis L. 89841–89843.

63. CRASSULACEAE

- Crassula natans* Thunb. var. *natans* 90061.
natans Thunb. var. *filiformis* (E. & Z.)
 Toelken 90060.

- Crassula decumbens* Thunb. var. *decumbens*
 90055.

- glomerata* L. 90056–90059; 90899.
thunbergiana Schult. ssp. *thunbergiana*
 90050–90053.
umbellata Thunb. 90054.
pellucida L. ssp. *pellucida* 90041.
capensis (L.) Baill. var. *capensis* 90042–
 90043.
cymosa Berg. 90047; 90048.
flava L. 89829–89835.
nudicaulis L. var. *nudicaulis* 90044.
fallax Friedr. 90049.
strigosa L. 90045; 90046.

64. SAXIFRAGACEAE

- Montinia caryophyllacea* Thunb. 89861–
 89863.

66. BRUNIACEAE

- Staavia radiata* Dahl 89848; 89849.
Berzelia abrotanoides Brongn. 89846;
 89847.

67. ROSACEAE

- Alchemilla capensis* Thunb. 90039; 90040.
Cliffortia falcata L.f. 90028–90031.
obcordata L.f. 90023; 90024.
stricta H. Weimarck 90898.
juniperina L.f. 90021; 90022.
filifolia L.f. 90018–90020.
polygonifolia L. 90032–90035.
strobilifera Murr. 90025; 90026.
ferruginea L.f. 90027.
Rubus pinnatus Willd. 90038.
fruticosus L. 90036; 90037.

68. LEGUMINOSAE

- Podalyria calypttrata* Willd. 89697; 89698.
calypttrata Willd. x *cuneifolia* Vent.
 89896.
biflora (Retz.) Lam. 89699; 89700.
sericea R. Br. 89701–89703.
cuneifolia Vent. 89694; 89695.
Virgilia oroboides (Berg.) Salter 89955;
 89956.
Amphithalea ericifolia (L.) E. & Z. 89670.
Liparia splendens (Burm. f.) J. J. Bos & de
 Wit 89704.
Priestleya sericea (L.) E. Mey. 89669.
Rafnia capensis (L.) Druce 89876; 89674;
 89671.
angulata Thunb. 89672; 89673; 89675.
triflora Thunb. 89677–89679.

- Crotalaria capensis* Jacq. 89937.
Lotononis peduncularis Benth. 89690; 89691.
 **Cytisus candicans* Lam. 89938.
Lebeckia carnosa (E. Mey.) Druce 89687; 89688.
meyeriana E. & Z. 89689.
Aspalathus cordata (L.) R. Dahlgr. 89680.
angustifolia (Lam.) R. Dahlgr. 89681–89683.
linearis (Burm. f.) R. Dahlgr. ssp. *linearis* 89684–89686.
Psoralea pinnata L. 89898–89903.
fruticans (L.) Druce 89888–89891.
decumbens Ait. 89892–89895.
fascicularis DC. 89897.
capitata L.f. 89896.
aphylla L. 89904–89906.
alata (Thunb.) Salter 89885.
laxa Salter 89886; 89887.
imbricata (L.) Salter 89882–89884.
 **Trifolium campestre* Schreb. 89911; 89912.
 **dubium* Sibth. 89913; 89914.
 **angustifolium* L. 89907–89909.
burchellianum Ser. 89915; 89916.
 **Medicago polymorpha* L. 89932.
 **Melilotus indica* All. 89910.
Indigofera cytisoides Thunb. 89933–89935.
mauritanica (L.) Thunb. 89924–89926.
capillaris Thunb. 89917–89919.
angustifolia L. 89920–89923.
psoraleoides L. 89927.
incana Thunb. 89928–89931.
Sutherlandia frutescens (L.) R. Br. 89939; 89940.
Lessertia capensis (Berg.) Druce 89941.
herbacea (L.) Druce 89942; 89943.
 **Lathyrus latifolius* L. 89952; 89953.
 **Vicia sativa* L. 89945.
angustifolia Roth 89946.
hirsuta (L.) S. F. Gray 89948.
tetrasperma (L.) Moench 89949; 89950.
atropurpurea Desf. 89947.
varia Host. 89951.
Rhynchosia capensis (Burm.) Schinz 89954.
Bolusafrá bituminosa (L.) Kuntze 89944.
Dipogon lignosus (L.) Verdc. 89936.
69. GERANIACEAE
 **Geranium dissectum* L. 89521.
Pelargonium marginatum R. Knuth 89516; 89517.
longifolium (Burm. f.) Jacq. 89518–89520.

- Pelargonium triste* (L.) Ait. 89515; 89530.
myrrhifolium (L.) Ait. 89529; 89531.
alchemilloides (L.) Ait. 89528.
chamaedriforme Jacq. 89526.
grossularioides (L.) Ait. 89527.
cucullatum (L.) Ait. 89533.
capitatum (L.) Ait. 89532.
betulinum (L.) Ait. 89525.
 **Erodium moschatum* L'Her. 89522–89524.

70. OXALIDACEAE

- Oxalis pes caprae* L. 89539; 89540.
compressa L.f. 89538.
dentata Jacq. 89547.
incarnata L. 89588.
lanata L.f. 89541–89544.
obtusata Jacq. 89565–89569.
luteola Jacq. 89545; 89546.
bifida Thunb. 89548.
purpurea L. 89589; 89595–89607.
punctata L.f. 89608–89610.
depressa E. & Z. 89549.
eckloniana Presl var. *sonderi* Salter 89591; 89592.
hirta L. 89550–89553.
nidulans E. & Z. var. *nidulans* 89590; 89593; 89611; 89581; 89582; 89584; 89585.
nidulans E. & Z. var. *denticulata* (W. Dod) Salter 89586; 89587.
commutata Sond. 89580.
glabra Thunb. 89534–89537; 89612–89615.
versicolor L. 89570–89579.
polyphylla Jacq. 89554–89560; 89562; 89563.

71. LINACEAE

- Linum africanum* L. 89503.
 **usitatissimum* L. 89502.

72. ZYGOPHYLLACEAE

- Zygophyllum sessilifolium* L. 89501.

73. RUTACEAE

- Diosma hirsuta* L. 89821; 89822; 89825–89827.
oppositifolia L. 89818–89820; 89823; 89824; 89828.
Adenandra villosa (Berg.) Licht. ex Roem. & Schultes var. *biseriata* (Mey. ex Bartl. & Wendl.) Strid 89814.
Macrostylis villosa (Thunb.) Sond. 89813; 89815–89817.

Agathosma imbricata (L.) Willd. 89804–89808.
glabrata Bartl. & Wendl. 89803; 89809–89812.

74. POLYGALACEAE

Polygala myrtifolia L. 89429.
garcini DC. 89431–89436.
refracta DC. 89430.
Nylandtia spinosa (L.) Dumort 89487–89491.
Muraltia heisteria (L.) DC. 89423; 89634; 89492–89496.
filiformis (Thunb.) DC. 89414; 89419; 89420.
ericoides (Burm. f.) Steud. 89498–89500.
? alopecuroides (L.) DC. 89497.
thymifolia (Thunb.) DC. 89415–89418; 89422.
thunbergii E. & Z. 89424–89428.
brevicornu DC. 89421.

75. EUPHORBACEAE

**Euphorbia peplus* L. 90828; 90829.
helioscopia L. 90826; 90827.
erythrina Link 90821; 90822.
tuberosa L. 90823–90825.
Clutia alaternoides L. 90830.
 **Mercurialis annua* L. 89751; 89752.

76. ANACARDIACEAE

Rhus rosmarinifolia Vahl 89617–89620.
angustifolia L. 89616.
angustifolia L. x *rosmarinifolia* Vahl 89621; 89622.
tomentosa L. 89623–89625.
laevigata L. 89644–89652.
glauca Desf. 89627–89629.
lucida L. 89626; 89630–89632.

77. CELASTRACEAE

Maytenus heterophylla (E. & Z.) N. Robson 89653–89654.
oleoides (Lam.) Loes. 89655–89657; 89668.
Pterocelastrus tricuspidatus (Lam.) Sond. 89659–89663.
Cassine peragua L. 89658.

82. RHAMNACEAE

Phytolacca cephalantha Sond. 89667.
imberbis Berg. 89664–89666.
plumosa L. 89640–89643.
parviflora Berg. 89635–89637.
stipularis L. 89639; 89638.

85. MALVACEAE

**Malva parviflora* L. 89473.
 **Lavatera cretica* L. 89633.
Anisodonteia scabrosa (L.) Bates 89514.
Hibiscus aethiopicus L. 89512.
 **diversifolius* Jacq. 89510; 89511.
 **trionum* L. 89513.

86. STERCULIACEAE

Hermannia althaeifolia L. 89504.
cuneifolia Jacq. var. *cuneifolia* 89505–89507.
lacera Fourcade 89508; 89509.

91. VIOLACEAE

**Viola arvensis* Murr. 89439.

92. FLACOURTIACEAE

Kiggelaria africana L. 89437; 89438.

93. PENAEACEAE

Penaea mucronata L. 90817; 90818.
Stylapteris fruticosus (L.f.) A. Juss. 89692; 89693.

95. THYMELAEACEAE

Gnidia laxa (L.f.) Gilg 90780–90782.
inconspicua Meisn. 90800; 90801.
nana (L.f.) Wikström 90799.
pinifolia L. 90793; 90794.
viridis Berg. 90788–90792; 90795–90798.
Struthiola striata Lam. 90810–90812.
dodecandra (L.) Druce 90813–90816.
ciliata (L.) Lam. 90802–90809.
Lachnaea capitata (L.) Meisn. 90786; 90787.
Cryptadenia uniflora (L.) Meisn. 90784; 90785.
Passerina vulgaris Thoday 90783.

96. LYTHRACEAE

Lythrum hyssopifolia L. 89859.

98. OENOTHERACEAE

Epilobium tetragonum L. 89860.
 **Oenothera affinis* Camb. 93384.
 **erythrosepala* Borbás 93381.
 **indecora* Cambess. ssp. *bonariensis* Dietr. 93387.
 **longiflora* L. 93382; 93383.
 **parviflora* L. 93386.
 **stricta* Ledeb. ex Link 93385.

99. HALORHAGACEAE

- Gunnera perpensa* L. 89853–89858.
Lauremburgia repens Berg. 89850–89852.

101. UMBELLIFERAE

- Centella coriacea* Nannfd. 89957.
tridentata (L.f.) Druce 89958–89961.
glabrata L. 89962.
macrocarpa (Rich.) Adamson 89963–89968.
Arctopus echinatus L. 89969–89971.
Torilis arvensis (Huds.) Links 90408; 90409.
Lichtensteinia lacera Cham. & Sch. 89978–89981; 90415–90417.
beiliana Eck. & Zeyh. 89973–89977; 90418.
Sonderina hispida (Thunb.) Wolff 89972; 89982.
Thunbergiella filiformis (Lam.) Wolff 89983–90006; 90412; 90413.
**Foeniculum vulgare* Mill. 90414.
Annesorrhiza capensis Ch. & Sch. 90007–90017.
Peucedanum sieberianum Sond. 90410; 90411.
Umbelliferae seedlings 90391; 90392.

103. ERICACEAE

- Erica plukenetii* L. 90419; 90455.
cerinthoides L. 90423; 90424.
mammosa L. 90420; 90421; 90423.
mauritanica L. 90446.
subdivaricata Berg. 90432–90434.
ferrea Berg. 90429; 90447; 90448.
nudiflora L. 90049.
viscaria L. 90428.
decora Andr. 90427.
pulchella Houtt. 90430; 90431.
lasciva Salisb. 90452–90454.
imbricata L. 90450; 90452.
corifolia L. 90456–90458.
baccans L. 90425; 90426.
Philippia chamissonis Kl. 90441.
Blaeria ericoides L. 90435.
Syndesmanthus articulatus (L.) Kl. 90436; 90437.
Salaxis flexuosa Kl. 90442–90445.
Scyphogyne muscosa (Ait.) Druce 90438–90440.

104. MYRSINACEAE

- Myrsine africana* L. 90730–90734.

105. PRIMULACEAE

- *Anagallis arvensis* L. 90716–90719.

108. EBENACEAE

- Diospyros whyteana* (Hiern.) F. White 90725.
glabra (L.) De Winter 90720–90724.
Euclea racemosa Murr. 90726–90729.

109. OLEACEAE

- Olea capensis* L. 90347–90350.
exasperata Jacq. 90343.
africana Mill. 90344–90346.

111. GENTIANACEAE

- Sebaea aurea* (L.f.) R. & S. 90355–90365.
schlechteri Schinz 90352.
micrantha (Cham. & Schlecht.) Schinz var. *micrantha* 90354.
micrantha (Cham. & Schlecht.) Schinz var. *intermedia* (Cham. & Schlecht.) Marais 90366.
exacoides (L.) Schinz 90351; 90353.
Orphium frutescens (L.) E. Mey. 90375–90378.
Chironia baccifera L. 90367–90369.
linoides L. ssp. *emarginata* (Jarosz) Verdoorn 90370–90374.

113. ASCLEPIADACEAE

- Microlooma tenuifolium* (L.) K. Schum. 90735; 90736.
Schizoglossum aschersonianum Schltr. 90737–90740.
Asclepias crispa Berg. 90749–90752.
cancellata Burm. 90757–90759.
fruticosa L. 90753–90756.
Cynanchum africanum R. Br. 90747; 90748.
Eustegia minuta R. Br. 90741–90746.

114. CONVULVULACEAE

- Cuscuta nitida* E. Mey. ex Choisy 90645–90650.
 sp. 90651.

115. BORAGINACEAE

- Lobostemon trichotomus* (Thunb.) DC. 90638–90640.
fruticosus (L.) Buek 90641–90644.

116. VERBENACEAE

- Stilbe ericoides* L. 90777–90779.
**Verbena bonariensis* L. 90775; 90776.

117. LABIATAE

- Salvia africana* L. 89783.
chamelaegnea Berg. 89782.
Stachys aethiopica L. 89788; 89789.
 **arvensis* L. 89784–89787.
Leonotis leonurus R. Br. 89790; 89791.

118. SOLANACEAE

- Lycium afrum* L. 90652–90660.
 **Datura stramonium* L. 90661–90664.

119. SCROPHULARIACEAE

- **Verbascum virgatum* Stokes 90637.
Hemimeris montana L.f. 90634–90636.
Diascia nemophiloides Benth. 90626.
Nemesia barbata (Thunb.) Benth. 90631–90633.
pinnata (L.f.) E. Mey. ex Benth. 90627; 90628.
versicolor E. Mey. ex Benth. 90629; 90630.
Polycarena heterophylla (L.f.) Levyns 90588; 90599.
Sutera tristis (L.f.) Hiern 90622; 90623.
Manulea tomentosa L. 90619–90621.
 **Veronica tournefortii* K. C. Gmelin 90624; 90625.
Alectra sessiliflora (Vahl) Kuntze 90612–90615; 90617.
Bartsia trixago L. 90610.
Harveya capensis Hook. 90618.
Hyobanche sanguinea L. 90611.
 **Orobanche ramosa* L. 90609.

120. SELAGINACEAE

- Selago corymbosa* L. 90593–90596.
spuria L. 90590–90592.
Microdon capitatus (Berg.) Levyns 90602.
Dischisma capitatum (Thunb.) Choisy 90597.
ciliatum (Berg.) Choisy 90598–90601.
Hebenstreitia dentata L. 90603–90606.

122. MYOPORACEAE

- Oftia africana* (L.) Bocq. 90607; 90608.

123. PLANTAGINACEAE

- **Plantago major* L. 89792–89794.
lanceolata L. 89795–89799.

124. RUBIACEAE

- Anthospermum aethiopicum* L. 90324–90330.
bergianum Cruse 90331–90334.

- Anthospermum prostratum* Sond. 90322; 90323.
ciliare L. 90335–90339.
Nenax acerosa Gaertn. 90340–90342.

125. DIPSACACEAE

- Scabiosa columbaria* L. 90531–90533.

127. CUCURBITACEAE

- Zehneria scabra* (L.f.) Sond. 89869; 89869.

128. CAMPANULACEAE

- Prismatocarpus fruticosus* L'Herit. 90692.
sessilis Eckl. ex A. DC. 90691.
Roella ciliata L. 90698–90704.
prostrata E. Mey. ex A. DC. 90693–90697.
Microdon glomeratum A. DC. 90705–90715.
Wahlenbergia capensis (L.) A. DC. 90683–90686.
cernua (Thunb.) A. DC. 90681; 90682.
procumbens (L.f.) A. DC. 90678–90680.
exilis A. DC. 90687; 90690.
 ? *subpilosa* von Brehm. 90688; 90689.
Lightfootia subulata L'Herit. 90670–90672.
longifolia A. DC. 90665–90669.
Cyphia bulbosa (L.) Berg. 90673–90677.
Laurentia secunda (L.f.) Kuntze 90307–90311.
arabidea (Presl) A. DC. 90306.
Monopsis simplex (L.) E. Wimm. 90312; 90313.
lutea (L.) Urban 90317–90321.
Lobelia coronopifolia L. 90294–90298.
setacea Thunb. 90303; 90304.
comosa L. 90287–90290.
alata Labill. 90305.
erinus L. 90299–90302.
depressa L.f. 90291–90293.
Grammatotheca bergiana (Cham.) Presl 90314–90316.
129. COMPOSITAE
- Corymbium glabrum* L. 90526.
africanum L. 90527–90530.
Felicia fruticosa (L.) Nichols 90523–90525.
 **Conyza ambigua* DC. 90520–90522.
ivaefolia (L.) Less. 90518; 90519.
Chrysocoma coma-aurea L. 90511.
Ifloga seriphioides (Berg.) Bol. & Wolley Dod 90509; 90510.
Gnaphalium candidissimum Lam. 90480–90484.
 **luteo-album* L. 90476–90479.

- Helipterum gnaphaloides* (L.) DC. 90508.
Helichrysum indicum (L.) Grierson 90501; 90502.
 rutilans (L.) Don 90505–90507.
 asperum (Thunb.) Hilliard & Burt 90503; 90504.
 serpyllifolium (Berg.) Pers. 90499; 90500.
 foetidum (L.) Moench 90498.
 cymosum (L.) D. Don 90496; 90497.
 niveum (L.) Less 90488–90490.
 maritimum (L.) D. Don ex G. Don 90491; 90492.
 teretifolium (L.) Sweet 90493; 90494.
 helianthemifolium (L.) D. Don 90485–90487.
 patulum (L.) D. Don 90495.
Leontonyx glomeratus (L.) DC. 90517.
Petalacte coronata (L.) D. Don 90515; 90516.
Stoebe plumosa (L.) Thunb. 90459–90461.
 capitata Berg. 90462–90464.
 fusca (L.) Thunb. 90465–90470.
Disparago lasiocarpa Cass. 90474; 90475.
Elytropappus gnaphaloides (L.) Levyns 90513.
 rhinocerotis (L.f.) Less. 90512.
Metalasia muricata (L.) Don 90278–90282.
 brevifolia (Lam.) Levyns 90274; 90275.
 cephalotes (Thunb.) Less. 90276; 90277.
Pulicaria scabra (Thunb.) Druce 90471.
Osmitopsis asteriscoides (Berg.) Less. 90472.
 **Bidens pilosa* L. 90473.
Athanasia dentata L. 90284.
 crithmifolia L. 90285; 90286.
 trifurcata L. 90283.
Eroeda capensis (L.) Levyns 90271–90273.
Pentzia suffruticosa (L.) Hutch. ex Merxm. 90586.
Cotula turbinata L. 90581–90585.
Senecio littoreus Thunb. 90268; 90269.
 abruptus Thunb. 90265–90267.
 arenarius Thunb. 90251; 90252.
 purpureus L. 90250; 90263.
 erosus L.f. 90264.
Senecio cymbalariifolius (L.) Less. 90270
 pubigerus L. 90237–90239.
 rigidus L. 90255; 90256.
 rosmarinifolius L.f. 90257; 90258; 90262.
 halimifolius L. 90253; 90254.
 burchellii DC. 90248; 90249; 90260; 90261.
 foeniculoides Harv. 90259.
 pinifolius (L.) Lam. 90240–90242.
 triqueter Less. 90243–90247.
Gymnodiscus capillaris (L.f.) Less. 90587; 90588.
Castalis nudicaulis (L.) T. Norl. 90234–90236.
Othonna filicaulis Jacq. 90575–90577.
 digitata L.f. 90572.
 bulbosa L. 90573; 90574.
 stenophylla Levyns 90578–90580.
 quinquedentata Thunb. 90569–90571.
Osteospermum imbricatum L. 90567.
 dentatum Burm. f. 90568.
Chrysanthemoides moniliferum (L.) T. Norl. 90565; 90566.
Ursinia chrysanthemoides (Less.) Harv. 90562.
 anthemoides (L.) Poir. 90563; 90564.
Arctotheca calendula (L.) Levyns 90561.
Arctotis acaulis L. 90558.
 breviscapa Thunb. 90559.
 angustifolia L. 90560.
Gazania pectinata (Thunb.) Spreng. 90557.
Berkheya armata (Vahl) Druce 90553; 90554.
 rigida (Thunb.) Bolus & Wolley Dod 90555; 90556.
 **Centaurea melitensis* L. 90551; 90552.
Gerbera piloselloides (L.) Cass. 90547.
 crocea (L.) O. Kuntze 90548–90550.
 **Cichorium intybus* L. 90545.
 **Hypochoeris radicata* L. 90544.
 **glabra* L. 90539–90543.
 **Urospermum picroides* F.W. Schmidt 90546.
 **Sonchus asper* Hill 90537; 90538.
 **oleraceus* L. 90534–90536.

ALOE MEYERI VAN JAARSVELD: A NEW ALOE FROM THE NORTH-WEST CAPE (R.S.A.)*

E. J. VAN JAARSVELD

(National Botanic Gardens of South Africa, Kirstenbosch)

ABSTRACT

A new *Aloe* species (Liliaceae) is described from the north-western Cape.

UITTREKSEL

ALOE MEYERI VAN JAARSVELD: 'N NUWE ALOE VANAF NOORD-WES KAAP (R.S.A.)

'n Nuwe *Aloe*-soort (Liliaceae) vanaf noordwes-Kaap word beskryf.

Aloe meyeri E. J. van Jaarsveld, sp. nova.; a *A. mitriformis* Miller differt, statura parva, habitu pendulo, foliis lanceolatis-acuminatis, inflorescentia simpliciter pendula-recurva, et floribus subclavatis dimidio minoribus.

Type: South Africa: Cape Province—2817 (Tatasberg): Rosyntjieberg, 500 m south of Devil's Tooth (-AD), *van Jaarsveld 6137* (NBG, holo.!).

Plants hanging from vertical south-facing cliffs. *Stems* up to 1 m long, up to 40 mm in diam., grey; old stems longitudinally fissured; simple or branched from the base or sometimes with offshoots along stem; only apical part foliated. *Rosette* up to 26 mm in diam., hanging downwards and not ascending, old dry leaves persistent for a short length. *Leaves* glaucous, narrowly lanceolate acuminate up to 200 mm long and 35 mm in diam., erectly spreading, sometimes reddish-brown tinged, leathery, rosulate and basally sheathing, upper and lower surface striate at base, upper surface slightly channelled at base, more distinctly so towards the apex. Lower surface obscurely keeled towards the apex. Margins armed with small white deltoid teeth 2×1 mm, 5-8 mm apart. Leaf sap drying orange-yellow. *Inflorescence* simple or rarely branched 150-250 mm long, pendulous-recurved. Peduncle 5 mm wide at base, cylindrical with few sterile deltoid scarious acuminate bracts 4 mm wide at base and up to 10 mm long; raceme capitate, rounded ± 70 mm long and ± 80 mm in diam., the buds orange-red, green-tipped, horizontally spreading to subpendulous, open perianth pendulous

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orange-red and green tipped. Bracts deltoid acuminate 3×5 mm. Pedicel 20 mm long. *Perianth* 20 mm long, cylindrical, subclavate slightly curved; obtuse to subacute at base, 3.5 mm in diam., proximally, widening to 4–5 mm near mouth; outer segments free to the base, apices subacute to obtuse, slightly spreading; inner segments much broader, subspathulate, apices rounded to subacute and spreading. Filaments yellow, the three inner lengthening before the three outer, flattened at base, up to 3 mm exerted beyond mouth. *Stigma* not protruding, or sometimes just exerted at mouth. *Ovary* green, 4 mm long and 2 mm wide.

Flowering period: December to February.



FIG. 1.

Aloe meyeri van Jaarsveld, sp. nov.

DISTRIBUTION

Confined to the Rosyntjieberg mountain-range in the north-east Richtersveld and just entering South West Africa. This interesting mountain-range runs east-west for approximately 25 km and just enters South West Africa in the east where *Aloe meyeri* also occurs on the mountain peaks east of Gorgons Head on the South West African side of the range.

HABITAT

It occurs on steep vertical south-facing upper slopes in crevices of quartzitic rock. The plants are scattered and not very common.



FIG. 2.
Aloe meyeri van Jaarsveld, sp. nov. Habitat.



FIG. 3. Inflorescence life size.

DISCUSSION

Aloe meyeri is most closely related to *Aloe mitriformis* Miller. It falls into the series Mitriformes (Reynolds, 1950) which includes *Aloe distans* Haw., *Aloe comptonii* Reynolds, *Aloe arenicola* Reynolds and *Aloe mitriformis* Miller.

This new aloe is at once distinguished from *Aloe mitriformis* by being a much smaller plant. The rosette is carried on the apical part of the stem and hangs downwards. The leathery leaves are lanceolate-acuminate and striate basally. The inflorescence is simple (rarely branched), and pendulous-recurved. The sub-

clavate corolla is shorter by half than in *Aloe mitriformis*. As with *A. mitriformis*, the leaves normally become drawn together in the dry season. According to present information, *A. meyeri* occurs only on the Rosyntjieberg mountain-range (north-west Cape) and is thus geographically isolated from *A. mitriformis* which is restricted to the south-west Cape.

This distinctive new aloe is named after the late Rev. G. Meyer of Steinkopf, who first collected it during September 1939, together with the late Mr. Hans Herre of Stellenbosch University. (*Aloe* Vol. II No. 1 pg. 18, March, 1973). The discovery was brought to the attention of the late Mr. N. S. Pillans and Dr. G. W. Reynolds but according to Hans Herre they considered its identity to be a hybrid, with *A. kapohliana* as a possible parent.

During the course of a collecting trip, on the 11th June 1980, together with Mr. Piet Drijhout of Stellenbosch, while in search of succulents and pelargoniums, the author inspected the upper south slopes of a quartz peak on the Rosyntjieberg and came across a population of this aloe and recognised it to be undescribed. Subsequently, the author came across an article by Hans Herre in *Aloe* (Vol. II No. 1 March, 1973) "Herinneringe van 'n besoek aan die Richtersveld", in which mention is made of the Rev. G. Meyer's prior discovery, in September, 1939, of the same aloe which is now described here as *Aloe meyeri*.

After our discovery on the 11th June, 1980, populations were found at several other localities on the Rosyntjieberg. John Patterson, a keen mountaineer and nature conservation student, found a population on the South West African side of the Rosyntjieberg, which is the most eastern distribution record.

The most northern record was established by Mr. Kobus Kritzinger, law enforcement officer at Springbok, for Cape Provincial Nature Conservation Department, who collected plants on Mount Terror, a northern outlier of the Rosyntjieberg.

Earlier this year the author, together with Mr. Deon Kotze of NBG, assisted by Mr. Piet van der Westhuizen and Mr. Kobus Kritzinger re-collected flowering material of the new aloe from which this account was prepared.

ACKNOWLEDGEMENTS

- (1) Dr. John Rourke is thanked for his help, encouragement and preparation of the Latin diagnosis.
- (2) Mr. John Winter for encouragement and allowing the author to be away on the various field trips to the Richtersveld.
- (3) Mr. Piet van der Westhuizen, Curator, Hester Malan Nature Reserve, Springbok, who very kindly took us with his Landrover and together with Mr. Kritzinger assisted in collecting the type material.

REFERENCES:

- REYNOLDS, G. W. 1974. The Aloes of South Africa. Cape Town/Rotterdam: Balkema.

NOTES ON THE GENUS *PELARGONIUM* (FAM. GERANIACEAE)

E. M. MARAIS, P. VORSTER and J. J. A. VAN DER WALT

(Department of Botany, University of Stellenbosch)

ABSTRACT

1. The new name *Pelargonium ellaphieae* E. M. Marais is designated for *P. marginatum* Knuth (1912), non (Cav.) Link (1822). 2. *P. ovato-stipulatum* Knuth is reduced to subspecific rank as *P. stipulaceum* subsp. *ovato-stipulatum* (Knuth) Vorster, comb. & stat. nov. 3. It is shown that *P. paniculatum* Jacq. which was previously typified by an illustration, can be typified by a specimen annotated by Jacquin. 4. The name *P. eberlanzii* has been applied independently to two different species. *P. eberlanzii* Dinter is a synonym of *P. sibthorpiifolium* Harv. of the section *Cortusina*, while *P. eberlanzii* Knuth belongs to the section *Otidia*. 5. The correct author citation for *P. antidysentericum* is (Eckl. & Zeyh.) Kostel. (1836) and not (Eckl. & Zeyh.) Harv. (1860).

UITTREKSEL

NOTAS OOR DIE GENUS *PELARGONIUM* (FAM. GERANIACEAE)

1. Die nuwe naam *Pelargonium ellaphieae* E. M. Marais word gegee aan *P. marginatum* Knuth (1912), non (Cav.) Link (1822). 2. *P. ovato-stipulatum* Knuth word 'n subspe-sie van *P. stipulaceum* (L.f.) Willd as *P. stipulaceum* subsp. *ovato-stipulatum* (Knuth) Vorster, comb. & stat. nov. 3. Daar word aangedui dat *P. paniculatum* Jacq. wat voorheen tipifiseer was deur 'n illustrasie, tipifiseer kan word deur 'n eksemplaar wat deur Jacquin annoteer is. 4. Die naam *P. eberlanzii* is in die verlede onafhanklik van mekaar toegepas op twee verskillende spesies. *P. eberlanzii* Dinter is 'n sinoniem van *P. sibthorpiifolium* Harv. van die seksie *Cortusina*, terwyl *P. eberlanzii* Knuth in die seksie *Otidia* hoort. 5. Die korrekte outeursituasie vir *P. antidysentericum* is (Eckl. & Zeyh.) Kostel. (1836) en nie (Eckl. & Zeyh.) Harv. (1860) nie.

VALIDITY OF THE NAME *PELARGONIUM MARGINATUM* KNUTH

The name *Pelargonium marginatum* (Cav.) Link (1822), based on *Geranium marginatum* Cav. [Diss. 4: 230 (1787)], was originally applied to a horticultural hybrid which probably involved *P. zonale* (L.) L' Hér. Knuth's use in 1912 of the name *P. marginatum* for a new species in the section *Seymouria* is therefore illegitimate. As no alternative name is available for the latter species, the following new name is chosen in honour of Mrs. Ellaphie Ward-Hilhorst, botanical artist dedicated to portraying all the natural species of *Pelargonium* in water colour:

***Pelargonium ellaphieae* E. M. Marais, nom. nov.**

P. marginatum Knuth in Pflanzenr. 4, 129: 351 (1912); non (Cav.) Link, Enum. Hort. Berol. 2: 189 (1822).

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Type: CAPE—"Am Fusse des Muizenberg," Bolus 8054 (Z., lecto., here selected!; BOL!, GRA!, K!, NH!, PRE!).

AFFINITIES OF *P. OVATO-STIPULATUM* KNUTH

P. ovato-stipulatum Knuth is morphologically similar to *P. stipulaceum* (L.f.) Willd., except for the persistent stipules which are considerably larger, ovate instead of triangular, and almost completely glabrous with more sparsely spaced glandular hairs compared to *P. stipulaceum*. In our opinion these differences do not warrant specific distinction, and as the name *P. stipulaceum* is the oldest, that is the correct name to apply. Nevertheless the two former species are easy to distinguish from each other on account of the morphology of the stipules, and as the two variants are geographically separated (Fig. 1), genetic isolation from each other is implied. For these reasons the relationship between them is considered to be subspecific, and accordingly the following new combination is made:

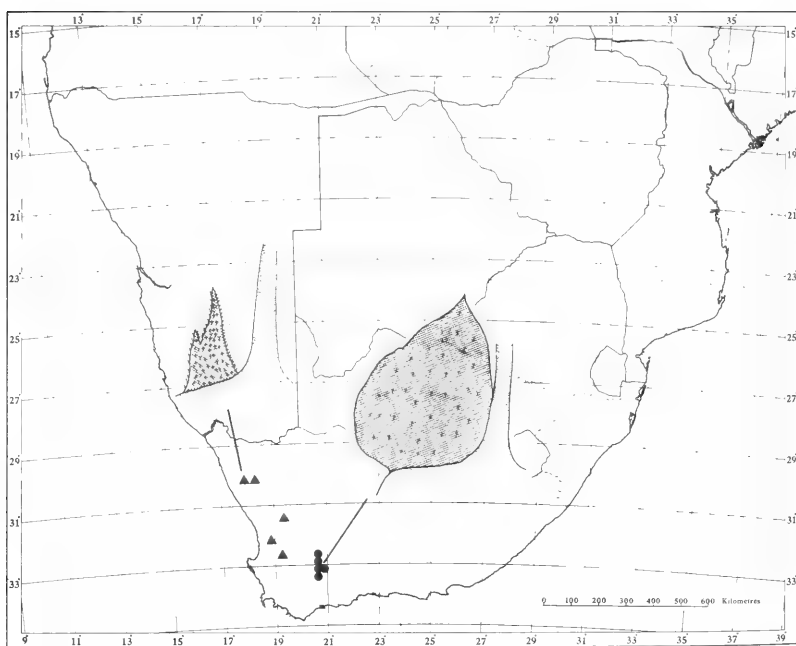


FIG. 1.

Pelargonium stipulaceum: known geographical distribution and shape of the stipules of the subsp. *stipulaceum* (▲) and *ovato-stipulatum* (●).

Pelargonium stipulaceum (L.f.) Willd. subsp. ***ovato-stipulatum*** (Knuth) Vorster, comb. & stat. nov.

P. ovato-stipulatum Knuth in Pflanzenr. 4, 129: 379, fig. 50B (1912). Type: CAPE—" . . . bei Matjesfontein . . .", MacOwan 1808 (G!, K!, SAM!, Z!).

subsp. ***ovato-stipulatum***

REPRESENTATIVE SPECIMENS

CAPE—3220 Sutherland: Verlatenkloof (-DA), Marloth 9624 (BOL!, PRE!); Sutherland: 47 miles south of (-DC), Leighton 3185 (BOL!).

— 3320: Matjesfontein (-BA), MacOwan 1808 (G!, K!, SAM!, Z!; type of *P. ovato-stipulatum* Knuth), Moffett 823 in STE-U 454 (STE-U!), Van der Walt 814 in STE-U 1621 (STE-U!); Whitehill (-BA), Barker 4872 (BOL!), Compton 3032 (BOL!), Leighton 255 (BOL!); Laingsburg (-BB), Van der Walt 807 in STE-U 1600 (STE-U!); Matjesfontein: foot of Witteberge (-BC), Marloth 11432 (PRE!).

subsp. ***stipulaceum***

REPRESENTATIVE SPECIMENS

CAPE—3017: Kamieskroon (-BB), Esterhuysen 23606 (BOL, 2 sheets!; PRE!).

— 3018: Kamiesberge: Leliefontein (-AB), Drège 3234 (PRE!); Leipoldt 3214 (BOL!).

—3119 Calvinia: Driefontein (-AD), Acocks 18617 (PRE!).

—3218: Clanwilliam (-BB), H. Bolus 8948 (BOL!).

—3219: between Grootrivier and Voëlfontein on road between Algeria Forestry Station and Ceres (-CB), Hugo 737 (PRE!, STE!).

TYPEFICTION OF *PELARGONIUM PANICULATUM* JACQ.

When re-instating *P. paniculatum* Jacq. after it had been regarded as a synonym of *P. crithmifolium* J.E. Sm. for almost 160 years. Merxmüller in Mitt. bot. StSamml., Münch 5: 240–241 (1964) designated the illustration which accompanied Jacquin's original description (Jacq., Hort. Schoenbr. 2: 6, t. 137 (1797)) as iconotype, since he was unable to trace any herbarium specimens suitable for lectotypification either in Jacquin's collection in W or elsewhere. It appears however that Merxmüller had overlooked the presence of a specimen of this species in W which has the name written on in Jacquin's own handwriting. While there is no proof that this specimen was not added after the publication of Hort. Schoenbr., we nevertheless consider this specimen to be a strong contender for a lectotype. Accordingly we here designate this specimen, without collector or number, as the lectotype of *Pelargonium paniculatum*, and we have labelled the specimen as such.

IDENTITY OF *P. EBERLANZII*

The name *P. eberlanzii* has been applied to two different species. The first occasion was in 1923 by Dinter (in *Reprim nov. Spec. Regni veg. (Beih.)* 23: 43). The description is rather informal and somewhat hidden in the text of the article, but it is nevertheless quite clear. Dinter neither cited specimens nor designated a type, but mentioned that the name commemorated the discoverer of the plant, Eberlanz. We traced specimens received by Dinter from Eberlanz and numbered *Dinter 3834* in BOL and PRE which match the description and are determined as *P. eberlanzii* in Dinter's handwriting. We consider these to be the type specimens of *P. eberlanzii* Dinter. Although Dinter assigned the species to the section *Hoarea*, these specimens match the species correctly known as *P. sibthorpiiifolium* Harv. of the section *Cortusina*.

In 1933 Knuth (in *Reprim nov. Spec. Regni veg.* 34: 147) described as new *P. eberlanzii* from specimens collected by Eberlanz and cultivated in the Botanical Garden in Berlin. No preserved specimens could be traced, but from the description it is clear that Knuth correctly assigned the species to the section *Otidia*. *P. eberlanzii* Knuth was stated to be closely related to *P. ferulaceum* (Burm. f.) Willd., which in turn appears to be part of the conglomeration of taxa which conveniently are being grouped together under the name *P. carnosum* (L.) L' Hérít.

Thus, *Pelargonium eberlanzii* Dinter is placed in synonymy under *P. sibthorpiiifolium* Harv., while *P. eberlanzii* Knuth, which is in any case an illegitimate later homonym, is reduced to synonymy under *P. carnosum* (L.) L' Hérít.

CORRECT AUTHOR CITATION FOR *P. ANTIDYSENTERICUM*

In the latest taxonomic treatment of *Pelargonium*, that by Knuth in *Pflanzenr.* 4, 129 (1912), the authority for *P. antidysentericum* is cited (p. 391) as (Eckl. & Zeyh.) Harv. [in *Fl. Cap.* 1: 286 (1860)]. The epithet *antidysentericum* has however been transferred earlier to the genus *Pelargonium* by Kosteletsky, and therefore the correct citation is:

Pelargonium antidysentericum (Eckl. & Zeyh.) Kostel., *Allg. Med.-Pharm. Flora* 5: 1896 (1836).

SHORT NOTE

LILIACEAE: SOME NAME CHANGES IN THE *URGINEAE* COMPLEX

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In Optima Leaflets from the Landesmuseum of Linz, Austria, **104**: 193–237 (1980) Speta referred to three old generic names described by Rafinesque in his *Flora Telluriana* **3**: 52–53, 60 (1837; as '1836'), which belong to the *Urgineae* complex but were overlooked until now.

Two of these, *Tenicroa* and *Pilasia* (1837), are congeneric with *Sypharissa* Salisb. (1864), which becomes a synonym. Speta selected the genus *Tenicroa* Rafin. and placed *Pilasia* Rafin. as a synonym of it.

Herewith the four species of the genus:

1. ***Tenicroa fragrans*** (Jacq.) Rafin., Flor. Tell. **3**: 52 (1837 as '1836'); Speta in Optima Leaflets **104**: 195 (1980). Type species of genus. The name *Tenicroa*, translated as 'coloured ribbon' by Rafinesque, refers to the banded cataphylls.
Anthericum fragrans Jacq., Hort. Schoenbr. 1, t. 86 (1797), basionym.
Sypharissa fragrans (Jacq.) Salisb. ex Oberm. in Bothalia **13**: 113 (1980). For further synonymy consult the latter publication.
2. ***Tenicroa exuviata*** (Jacq.) Speta in Optima Leaflets **104**: 195 (1980).
Anthericum exuviatum Jacq., Icon. **2**: 18, t. 415 (1794), basionym. *Sypharissa exuviata* (Jacq.) Salisb. ex Oberm. in Bothalia **13**: 113 (1980).
3. ***Tenicroa filifolia*** (Jacq.) Oberm., comb. nov.
Anthericum filifolium Jacq., Icon. Pl. Rar. **2** (8): t. 414 (1794), basionym.
Pilasia filifolia (Jacq.) Rafin., Fl. Tell. **3**: 536 (1837). *Sypharissa filifolia* (Jacq.) Salisb. ex Oberm. in Bothalia **13**: 113 (1980).
4. ***Tenicroa multifolia*** (Lewis) Oberm., comb. nov.
Urginea multifolia Lewis in Ann. S. Afr. Mus. **40**: 9 (1952), basionym.
Sypharissa multifolia (Lewis) Oberm. in Bothalia **13**: 114 (1980).

The third genus, *Strepsiphyla* Raf., Fl. Tell. **3**: 60 (1837), was based on *Drimia villosa* Lindl. in Bot. Reg. t. 1346 (1830). Rafinesque believed to have observed that the tepals were of unequal length and he therefore described it as a new genus. However, all are equally long. The name is rejected.

Mr. O. Kerfoot of the Botany Department of the University of the Witwatersrand, drew my attention to the publication from the Landesmuseum of Linz, Austria, for which I thank him sincerely.

Accepted for publication 30th April, 1981.

BOOK REVIEWS

SEEDLINGS OF DICOTYLEDONS, by E. F. de Vogel, with pp. 471. ISBN 90-220-0694-4. Wageningen: Centre for Agricultural Publishing and Documentation, 1980. P.O. Box 4, 6700 AA Wageningen, Netherlands. Dfl. 150.

This book is the result of a three year research project by the author in Indonesia. The project was sponsored by the Netherlands Universities Foundation for International Co-operation.

The first part of the book deals with the structure and diversity of seedlings while attention is also given to seedling terminology and in the historical review valuable references to older and other relevant literature are given. The term 'paracotyledons' which is used for "exposed, thin, green, leaflike, assimilating, 'cotyledons'" might be somewhat premature since insufficient evidence is supplied to justify the distinction between 'true cotyledons' and 'paracotyledons'.

The second part of the text deals with the classification of seedling types. A key to the different types, a semophyletic model showing hypothetical pathways of derivation between the different seedling types and subtypes, as well as detailed descriptions of the 16 different seedling types are given. Chapters pointing out the significance of seedlings in taxonomy and ecology are also included. This part, like the rest of the book, is well illustrated.

The last part consists of detailed descriptions of 150 different seedlings. Each description is illustrated with excellent black and white drawings. References to generic descriptions and distribution are also given. The 20 superb colour plates contribute to the attraction and quality of this book as do the 175 × 245 mm cloth cover and the quality of the paper.

As a whole this book is a valuable contribution to the knowledge of seedlings and the fact that so many South African plant families are represented, makes it a useful publication for local botanists. Although very useful and stimulating, the classification of seedlings in different types and subtypes must not be regarded as final since this work is primarily based on seedlings of tropical trees, whereas a more complete system can be expected once seedlings of all vegetation types are included.

The price of Dfl 150-00 is somewhat discouraging but one still buys good quality when purchasing this book.

P. J. ROBERTSE

FLORA OF NEW ZEALAND, Volume III, by A. J. Healy and E. Edgar, with pp. xlii + 220, 4 colour plates, 31 text figures and 4 maps. Wellington: P. D. Hasselberg, Government Printer, 1980. NZ \$18,50.

The very successful format of Vol. II, published ten years earlier, has been repeated in this volume. The attractive dust jacket, four maps on end papers, good quality paper, clear print and handy size, are all as before. Only the price shows an inflationary leap, from \$4,50 to \$18,50 New Zealand dollars.

A flora dealing almost entirely with adventives (aliens, "weeds") is surely unique. Historic reasons for such a segregation are explained in the preface. J. D. Hooker, in 1855, was so greatly alarmed at the rapidity with which European weeds were being introduced into New Zealand, that he decided to concentrate only on indigenous flora in his *Flora-Nova-Zelandiae*.

This present volume represents a transitional stage from the historic New Zealand treatment to the presently accepted one of including both native and adventive groups in floras.

This volume includes both indigenous and adventive "Cyperaceous, Petalous and Spathaceous Monocotyledons". As native species have already been dealt with in Vol. II, they get limited treatment here, apart from any additional information that may have come to light. A fourth volume will deal with Poaceae, hopefully in the not too distant future.

There is a chronological as well as a subject list of the *Annals of Taxonomic Research on New Zealand Plants* for the years 1969-76 (including earlier titles omitted in Volumes I and II). In addition there is a Bibliography of First Records of the appearance of each adventive species. The praiseworthy compilation of these records must have entailed a most diligent examination of relevant literature.

Keys to the families, genera and species, are clearly set out with well-contrasted numbered couplets. Families have been arranged, with some exceptions, according to Hutchinson's classification. Genera and species have been arranged alphabetically. There is also a useful key to families and some genera, based mainly on vegetative characters. Below the description of each alien species are notes on the country of origin and where the species was first recorded and collected in New Zealand.

The line drawings are excellent, if not abundant. South Africa's contribution to the more colourful adventives in New Zealand, is highlighted by the fact that of the 21 species photographed in colour, no less than 13 are from this country.

Unlike the two-way flow of aliens between Australia and South Africa, New Zealand seems to have suffered far more from plant immigrants from Africa than vice versa. South Africa's contribution to the flora is most noticeable in the family Iridaceae. Of 22 genera listed, only one is indigenous to New Zealand, whereas 17 are from South Africa. Recent name changes in South African Irids have been noted by the authors apart from the two most recent ones. *Gladiolus natalensis* is now *G. dalenii* Geel and *Watsonia ardernei* has been classed as a horticultural cultivar, *Watsonia pyramidata* 'Ardernei'. The only spelling mistake in the South African species is that of *Aponogeton distachyus*, which should have read *A. distachyos*.

The overall appearance, quality and accuracy are of the highest standard and this volume should be extremely useful to any agricuturist or botanist interested in the occurrence of weeds in the Southern Hemisphere.

PAULINE BOND

THREATENED PLANTS OF SOUTHERN AFRICA, South African National Scientific Programmes Report No. 45, by A. V. Hall, M. de Winter, B. de Winter and S. A. M. van Oosterhout, with pp. 244. ISBN 0-7988-1780-1. May 1980. Available on request from: C. S. P., C.S.I.R., P.O. Box 395, Pretoria, 0001, R.S.A.

The conservation of threatened plant species and their habitats have received rather limited attention in southern Africa to date perhaps partly because the extent and seriousness of the problem was not generally recognized even in conservation circles. This report makes a considerable contribution towards providing the necessary basic information. It represents the first attempt to assess the threatened plant problem in southern Africa, i.e. the region south of (but excluding) Angola, Zimbabwe and Mozambique.

The bulk of the report consists of lists of the 1915 vascular plant species (approximately 10% of the flora) which are considered by the authors to be either extinct or variously threatened in southern Africa. Three lists are provided, viz. an alphabetical list of threatened plant taxa within families, a list for each country or province (the latter in the case of the Republic of South Africa) and a list for each degree-square within each country or province. Conservation status categories which are equivalent to those used by the IUCN have been assigned to each species and a distinction is made between taxa endemic and non-endemic to the area in question. In addition these lists are cross-referenced by a comprehensive index.

Only a very general attempt is made at analysing the pattern of the threatened plant species problem but the overall pattern is clearly illustrated by tables and a map. The

analysis reveals a particularly high concentration of threatened plant taxa in the Cape Floristic Kingdom ($< 1\%$ of the area of southern Africa but with 65% of the threatened species) with other concentrations in Namaqualand and the eastern parts of southern Africa with very low numbers in the interior of South Africa, Namibia and Botswana.

Particularly valuable and of general interest is the chapter on "conservation perspectives" which provides a brief but penetrating account of the rationale for the theory and practice of the conservation of biotic diversity. Conservation strategies that will be necessary to conserve the diversity of the rich southern African flora are discussed and special attention is given to the much neglected aspect, the conservation of intra-specific genetic diversity.

Although the procedures that were followed in compiling the lists are briefly described (mainly reference to herbarium collections and recent revisions) no indication is given of the criteria which were used in the initial selection of species for inclusion in the list. The IUCN conservation status categories could not have been used as a basis for assessment in most cases since the status would not be apparent from herbarium records or from the literature for most species.

The preliminary nature of the report is stressed by the authors who ascribe this mainly to the immature state of the taxonomy of many groups and a lack of recent herbarium collecting for some groups and areas. However, the omission of many distinct and obviously rare species indicates that the selection process has not been as thorough as might have been expected.

The overall impression of this report is that of a carefully edited publication with remarkably few errors although some typographical errors and incorrect locality records were noted, for example *Protea lanceolata* is erroneously listed as occurring in the Caledon degree-square. A valuable reference list is provided which includes many important recent papers on threatened species conservation.

This report should be acquired by anyone interested in the conservation of the southern African flora and who has sufficient botanical knowledge to be able to make a contribution to a better understanding of the status and distribution of the listed species. By its very nature, however, this report would probably not reach as wide a circulation as the subject matter warrants. There is a definitive need for a summary report without the detailed species lists which would read a wider audience.

C. J. BURGERS

TRANSPORT IN PLANTS, by Ulrich Lüttge and Noe Higinbotham, with pp. x + 468, 1 portrait and 180 figures. ISBN 0-540-90383-6. Berlin, Heidelberg, New York: Springer-Verlag, 1979. US \$31.90.

This book has a pleasing appearance. The index is comprehensive and the subject matter is laid out clearly and logically. The authors' style is readable and explanations are presented lucidly so that even those who are not authorities in this field should have no difficulty in understanding concepts presented to them. This has also been achieved by the diagrams which are used freely to illustrate points in the text. The choice of picture on the cover is not good in that transport systems in hemiparasites and fungi do not appear to have received attention in this book. With the exception of the algae, the so-called lower plants have received scant attention, which is unfortunate in a book carrying a title purporting to cover a general field.

The book is divided into four parts. The first part deals with the biophysical background to this subject and the substances which are subject to transport. The chapter on biophysical background forms a useful start to the book, and the descriptions of the principles of the different mechanisms of transport contain sufficient mathematical detail to assist the reader in understanding the concepts without confusing him. The inclusion of a description of various techniques of measurement of relevant parameters is useful. In the third chapter the materials of transport are described, a section which also provides a good basis for understanding the information which follows.

Part II considers transport in relation to cell structure. Here the authors apply the principles elaborated in the early chapters to the situation as it actually exists in cells. There is a very pertinent section on the structure of cell walls and cell membranes. Structure is related to some of the mechanisms described in Chapter 2, and the characterization of carrier mechanisms, which follows on the description of membrane structure, is especially relevant. Several simplified cell models to explain transport mechanisms are reviewed objectively. Although there is experimental and computer evidence in support of the different models, it is made clear to the reader that much remains to be answered still. In Chapter 7 the authors attempt, by reference to specific cell organelles, to illustrate how various transport phenomena form an integral aspect of their physiology. Because of the direct association of transport mechanisms with the various organelles this was found to be a most interesting and informative section. In particular, the reviewer wishes to associate himself with the views expressed by the authors on the importance of active transport processes in transfer cells.

In Part III the authors deal with regulation and control of transport processes by cell metabolism. Respiration and photosynthesis are considered as sources for the provision of energy for active transport mechanisms. Here too the effects of phytochrome and plant hormones in regulating transport processes are also examined. Attention is also focused on the question of coupling between energy-providing reactions in mitochondria and chloroplasts and transport mechanisms at membranes spatially separated from these energy sources. To explain this coupling of energy with transport, biochemical and biophysical controls are considered. This section ties in well with the earlier chapter on the role of respiration and photosynthesis.

The final part describes inter-cellular and inter-organ transport. The occurrence and significance of apoplastic and symplastic transport pathways are examined here. Of special significance to the reviewer is a chapter which deals with correlations between transport processes within a plant as a whole. Because transport systems in cells, tissues and organs must be interdependent, the emphasis on the couplings and interconnections which occur, are welcomed. It is, however, unfortunate that in the short section dealing with salt exclusion in mangroves, a wider selection of references was not utilised. Despite this omission, the bibliography is fairly comprehensive.

This book should suit many tastes. While it is not suitable as an undergraduate textbook, it will be welcomed by specialists in this field and postgraduate students. Transport physiologists should be well pleased that an up-to-date, fairly comprehensive treatise on this subject has been published, while those with more general interests will also find this book most useful. At the price for which this book will sell in this country it represents good value for money and must find a place in all Botany departments.

T. D. STEINKE

GRADIENT MODELING: RESOURCE AND FIRE MANAGEMENT, by S. R. Kessell, with pp. xv + 432, 175 figures and 27 tables. ISBN 3-540-90379-8. Berlin, Heidelberg, New York: Springer-Verlag, 1979. DM 79,50. US \$43.80.

As Stephen R. Kessell was instrumental in developing the system of natural resource data banking which has now come to be known as "Gradient modeling", it is appropriate that he should be the author of this first full-length account.

In his own words, gradient modeling is "... the linkage of gradient analysis, vegetation models with site inventories and computer software to provide a natural resource information system". He gives three reasons for writing the book:— this is the first document to explain the detailed step-by-step development of such systems which he hopes will be of value to those considering the development of similar models for their own resource management problems and areas; it will provide advanced undergraduates, graduate students and field practitioners with a more detailed view of how resource information is gathered, compiled, stratified, stored and used to build resource management systems; and he hopes it will inspire other investigators to develop resource management models and systems through an open, interdisciplinary approach.

The author is largely successful in meeting these aims, reviewing the development of the system and bringing in appropriate ordination theory, as background, on which a large part of his system has been built. Two extant systems, the fire behaviour information integration system in Southern California and the fire management information system for the Northern Rocky Mountains, are described in detail and results of running the models are presented and discussed. Some four other related systems are described briefly.

The data gathering stage is described in full but the reviewer found the computer implementation chapter inadequate, considering that the system is dependent on a computer data banking system for operation. The short chapter of only nine pages merely lists the main subroutines, with one or two lines of description each, gives a simplified program flow chart and two pages of output. Considering the detail given in the rest of the book, this inadequacy is unfortunate. The reviewer would have preferred to have seen a complete computer program listing (or at least a listing of the main routines) instead of 144 pages of gradient population nomograms for Glacier National Park. A small subset of nomograms would have sufficed to illustrate the point made by the author as those given are of very little general interest.

To date, the successful models have been developed, under Kessell's guidance, in temperate North America and in the Californian chaparral, in both cases in well-understood vegetation. Kessell is presently attempting to implement a pilot system in New South Wales, Australia, which would be a good test of the portability of the system to data-poor parts of the world. The reviewer doubts that there is sufficient information available in South Africa to implement the system at present but its usefulness, particularly in the South-Western Cape, to conservation authorities is beyond question. The book itself is good for obtaining an idea of the scope of gradient modeling but inadequate for implementation of the system, should it be so desired, in South Africa.

J. W. MORRIS

SECONDARY PLANT PRODUCTS, edited by E. A. Bell and B. V. Charlwood, with pp. xvi + 674 and 176 figures. ISBN 3-540-09461-X. Berlin, Heidelberg, New York: Springer-Verlag, 1980. Volume 8 in "Encyclopaedia of Plant Physiology, New Series". DM 198. approx. US \$110.90.

This book, which is one of a series edited by A. Pirson and M. H. Zimmermann, is intended primarily for botanists. It does, however, have a very substantial chemical content and should prove to be a useful reference work for the organic natural product chemist.

The opening chapter deals with the historical development of the term, secondary plant products, and is followed by two chapters which examine the difficult problems of their phylogenetic and ecological significance, and the factors which control their production. The remainder of the volume is concerned initially with what are traditionally regarded as the major groups of secondary metabolites: alkaloids, terpenoids, steroids and plant phenolics, and then with groups such as non-protein amino acids, plant amines, cyanogenic glycosides, glucosinolates, betalains, plant lipids and plant carbohydrates.

Throughout the chapters information has been provided concerning the chemistry, biochemistry, taxonomic significance and probable ecological role of the groups of compounds, and in particular considerable attention has been paid to their biosynthesis. Mention is also made of exciting new techniques such as tissue culture, selective breeding and the artificial inducement of genetic changes. With so many topics to deal with it is inevitable that the coverage should be somewhat abridged. However, all the chapters are well referenced, the literature coverage in some cases extending to 1980.

Overall this is a well written book which should appeal to botanists and to the natural product chemist.

W. E. CAMPBELL

A FLORISTIC DESCRIPTION AND STRUCTURAL ANALYSIS OF THE PLANT COMMUNITIES OF THE PUNDA MILIA-PAFURI-WAMBIYA AREA IN THE KRUGER NATIONAL PARK, REPUBLIC OF SOUTH AFRICA:

3. THE *COLOPHOSPERMUM MOPANE* COMMUNITIES

N. VAN ROOYEN,* G. K. THERON AND N. GROBBELAAR

(Department of Botany, University of Pretoria)

ABSTRACT

The *Colophospermum mopane* communities of the Punda Milia-Pafuri-Wambya area in the Kruger National Park are described floristically and structurally. Habitat factors such as aspect, slope, soil, geology, altitude and pH of the soil are discussed briefly. The floristic classification of the communities was done by means of the Braun-Blanquet method and the communities are described in terms of the most conspicuous as well as the differential species in the woody and herbaceous strata. The structural analysis was done by means of the Variable Quadrant Plot method and the discussion of the structure of the communities is based on the different growth forms, their canopy spread in different strata and the number of individuals per hectare.

UITTREKSEL

'N FLORISTIESE BESKRYWING EN STRUKTURELE ANALISE VAN DIE PLANTGEMEENSAPPE VAN DIE PUNDA MILIA-PAFURI-WAMBIYA GEBIED IN DIE NASIONALE KRUGERWILDTUIN, REPUBLIEK VAN SUID-AFRIKA:

3. DIE *COLOPHOSPERMUM MOPANE* GEMEENSAPPE

Die *Colophospermum mopane* gemeenskappe van die Punda Milia-Pafuri-Wambya-gebied in die Nasionale Krugerwildtuin word aan die hand van hul floristiese samestelling en struktuur, wat onderskeidelik deur middel van die Braun-Blanquetmetode en die Varieerbare Kwadrantperseelmetode gemonster is, bespreek. Daar word kortliks na habitatkenmerke soos aspek, helling, grondkenmerke, geologie, hoogte bo seespieël en die pH van die grond verwys. Die floristiese klassifikasie van die verskillende gemeenskappe word aan die hand van die opvallendste en differensierende spesies van die houtagtige en kruidagtige stratus beskryf. Die strukturele beskrywing is veral op die verskillende groeivorme, hul kroonverspreiding in verskillende stratus en die aantal individue per hektaar gegrond.

INTRODUCTION

In the first paper of this series (Van Rooyen, Theron and Grobbelaar, 1981a) a general description was given of the location, topography, drainage, geology, soil and climate of the Punda Milia-Pafuri-Wambya area as well as a floristic description of the Hygrophilous communities. The second paper (Van Rooyen, Theron and Grobbelaar, 1981b) dealt with floristic and structural aspects of the Sandveld communities in the study area.

*Partly based on an M.Sc. thesis, University of Pretoria.

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METHODS

The non-statistical Braun-Blanquet method has been employed successfully in South Africa since 1969 (Taylor, 1969) and is accepted as a reliable and suitable method of vegetation classification. The Variable Quadrant Plot method (Coetzee & Gertenbach, 1977) which was developed in the Kruger National Park was used during this study to determine the species present, their trunk diameters, growth forms and height classes and to calculate their maximum canopy spread in different strata, total apparent canopy cover and number of individuals per hectare.

In this paper the *Colophospermum mopane* communities are described floristically according to the Braun-Blanquet method (Werger, 1973) and analysed structurally by the Variable Quadrant Plot method (Coetzee & Gertenbach, 1977). The descriptive phrase included in the name of each community is based on the physiognomic vegetation classification of Tinley (1969).

RESULTS AND DISCUSSION

The constancy table (Table 1) shows a number of species that are distributed over the entire area and therefore point out the affinities between the communities. Three main species groups (V, H and P) divide the Table into the Hygrophilous, the Sandveld and the *Colophospermum mopane* communities.

The *Colophospermum mopane* communities, which are characterised by species group P (Table 1), are found mainly on areas underlain by basalt and shale of the Karroo System as well as on the Malvernian Formation (Van Rooyen, 1978).

These communities can be divided into three main groups:

1. The *Colophospermum mopane*-*Euclea divinorum* tree savanna
2. The *Colophospermum mopane*-*Dalbergia melanoxylon*-*Heteropogon contortus* shrub savanna
3. The *Colophospermum mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna

The *Colophospermum mopane*-*Euclea divinorum* tree savanna (1) is characterised by species group K; the *Colophospermum mopane*-*Dalbergia melanoxylon*-*Heteropogon contortus* shrub savanna (2) by species group L and N, and the *Colophospermum mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna (3) by species groups O and P. The absence of a group of species, e.g. *Terminalia prunioides*, *Thilachium africanum*, *Acacia tortilis*, *Themedra triandra* and *Enneapogon scoparius* that occur in the other *Colophospermum mopane* communities, also serves to delineate this savanna (3).

The *Colophospermum mopane* communities are mutually related and gradual transitions from one community to another are often encountered. For example, the *Colophospermum mopane*-*Euclea divinorum*-*Enteropogon macrotachyus* tall

TABLE 1.

A constancy table of the plant communities of the Punda Milia—Pafuri—Wambiya area in the Kruger National Park*

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPERMUM MOPANE					4 DIABASE	HYGROPHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2		3	1.1	1.2	1.3	1.4
A	<i>Burkea africana</i>	5															
	<i>Fimbristylis hispidula</i>	3			1	1	1						1				
	<i>Andropogon gayanus</i>	3					1						1				
	<i>Holarrhena pubescens</i>	3															
	<i>Bauhinia galpinii</i>	3				1											
	<i>Ochna pulchra</i>	2		1													
B	<i>Baphia massaiensis</i>		5														
	<i>Grewia microthyrsa</i>		3														
	<i>Combretum celastroides</i>		3				1										
	<i>Hugonia orientalis</i>		3	1													
	<i>Ptaeroxylon obliquum</i>		2														
	<i>Pavetta catophylla</i>		2														
	<i>Cleistanthus schlechteri</i>		2														
	<i>Mariscus</i> sp.		2														
	<i>Heinsia crinita</i>	1	2														
	<i>Xylia torreana</i>		1														
C	<i>Xeroderris stuhlmannii</i>				3												
	<i>Aristida junciformis</i>	1		2													
	<i>Aristida stipitata</i>	1		3	1												
	<i>Indigofera inhambanensis</i>	1		2													
	<i>Limeum dinteri</i>			2	1									2			
	<i>Macrotyloma axillare</i>			2			1										
	<i>Pavonia burchellii</i>			2									1				
	<i>Balanites maughamii</i>		1	2		1								2			
D	<i>Terminalia sericea</i>	3	2	5	4												
	<i>Combretum collinum</i>	3	2	4	3	1								3			
	<i>Tricholaena monachne</i>	2	2	3	1	1			1	1	1		1				
	<i>Merremia tridentata</i>	4	3	3	3			1	1								
	<i>Crotalaria sphaerocarpa</i>	1	1	2	3	1			1			1	1				
	<i>Perotis patens</i>	3	3	3	3												
	<i>Pteleopsis myrtifolia</i>	3	3	2	1	1											
	<i>Eragrostis pallens</i>	2	4	2	2												
	<i>Zygoon graveolens</i>	1	2	3	3		1										
	<i>Aristida argentea</i>	2	2	1	1												

The constancy value of a plant species in a community is indicated by the following symbols: 1 (1–20 %); 2 (>20–40 %); 3 (>40–60 %); 4 (>60–80 %); 5 (>80–100 %)

*The complete differential table can be found in Van Rooyen (1978).

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2		3	4	1.1	1.2	1.3
H <i>Combretum zeyheri</i>	3	2	1	3	3	1											
<i>Borreria scabra</i>	1	2	3	1	1	2											
<i>Pogonarthria squarrosa</i>	4	2	2	3	2	1		1				2					
<i>Strychnos decussata</i>	1	2	1	1	1	1											
<i>Pseudolachnostylis maprounei</i> <i>folia</i>	5	1	1	2	2												
<i>Hexalobus monopetalus</i>	2	3	1	1	2												
<i>Strychnos madagascariensis</i> ...	3	2	4	3	3			1		3		1					
<i>Ipomoea magnusiana</i>	2	2	4	2		2	1	1				1					
<i>Guibourtia conjugata</i>	2	5	2		2												
<i>Rhynchosia resinosa</i>		2	3	1	2				1								
<i>Triumfetta pentandra</i>	1		1	2	1	2		1									
<i>Diplorhynchus condylocarpon</i> ..	4			1	3	1											
<i>Alchornea laxiflora</i>	1	4			2	1											
<i>Monodora junodii</i>	2	2		1	3	1											
<i>Celosia trigynia</i>	1	2			2	2		1									
<i>Waltheria indica</i>	2	2		2	3	1		1	1			2					
<i>Hymenocardia ulmoides</i>	2	2			3	1											
<i>Cassia absus</i>	1			2	1	1											
<i>Blepharis maderaspatensis</i> ...	1			1	2	2											
<i>Tephrosia elongata</i>	2	1	2	1	1			1									
<i>Rhynchosia venulosa</i>	1	1	2		1	1											
<i>Artabotrys brachypetalus</i>	1	1	1	1	2							1					
<i>Agathisanthemum bojeri</i>	2	2		1	1			1									
<i>Tephrosia longipes</i>	2		1	1	1							1					
<i>Crabbea velutina</i>	1		2		1	1		1					2				
<i>Hippocratea longipedunculata</i> ..		1	1	1	1												
<i>Ximenia caffra</i>	1			1													
<i>Ozoroa paniculosa</i>	1			1	1							1					
<i>Ozoroa engleri</i>			1	1													
I <i>Urochloa mosambicensis</i>				1			5	1		1	1	2		4	2		
<i>Chloris virgata</i>				1			4	1	1					2			
<i>Acacia tortilis</i>							3	1								1	
<i>Salvadora angustifolia</i>							2		1								
<i>Boerhavia diffusa</i>							2										1
<i>Azima tetraacantha</i>							2										
<i>Alternanthera pungens</i>							1										
<i>Trianthema triquetra</i>							1										
<i>Setaria verticillata</i>							1										
<i>Acacia senegal</i>					1		1										
<i>Cyathula crispula</i>							1										
J <i>Ximenia americana</i>			1	1			1	4									
<i>Enteropogon macrostachyus</i> ...					1	2	1	3	1								

PLANT SPECIES	COMMUNITIES																
	SANDVELD					COLOPHOSPERM MOPANE					DIABASE	HYGROPHILOUS					
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Tetrapogon tenellus</i>							1	2									
<i>Chloris roxburghiana</i>							1	2									
<i>Acacia grandicornuta</i>							2	1									
<i>Amaranthus thunbergii</i>							1	1									
K <i>Commiphora glandulosa</i>					1		2	1	3			1					
<i>Abutilon fruticosum</i>					1	1	2	2	2								
<i>Ecobolium revolutum</i>							2	2	2								
<i>Sporobolus smutsii</i>	1			1	1		2	1	1								
<i>Thilachium africanum</i>				1			2	1	1				2				
<i>Corbichonia decumbens</i>							1	1	2								
<i>Sporobolus fimbriatus</i>									1	1							
<i>Aristida rhinoclhoa</i>								1	1								
L <i>Enneapogon scoparius</i>										5							
<i>Euclea schimperi</i>				1						4							
M <i>Terminalia prunioides</i>							1	3	2	3							
<i>Maerua parvifolia</i>				2	1		3	3	2	1			2				
<i>Seddera capensis</i>							1	2	3	5	1	1					
<i>Elytraria acaulis</i>								2	2			1					
<i>Zanthoxylum capense</i>							1	1	2	2							
N <i>Themeda triandra</i>								1			5		2				
<i>Neorautanenia amboensis</i>								1	1		4						
<i>Setaria woodii</i>							1	1	1		3						
<i>Urochloa brachyura</i>								1			2						
<i>Panicum coloratum</i>											2		3				
O <i>Heteropogon contortus</i>	1				1			1	2	4	4	2	2		2		
<i>Bothriochloa insculpta</i>							1	2	3		4		2		2		
<i>Phyllanthus maderaspatensis</i> ..								1	2	2	1	1					1
<i>Fingerhuthia africana</i>								1	2	3	1	2					
<i>Indigofera heterotricha</i>								1	2	1	2	1					
<i>Sorghum versicolor</i>								1	2		3	1					
<i>Heliotropium strigosum</i>				2					2		2	1					
<i>Oropetium capense</i>								1	1	1	1	1					
P <i>Colophospermum mopane</i>				2	1		3	5	5	5	5	5		5	4		
<i>Euclea divinorum</i>	1			1			1	3	1	2		1		5	3		
<i>Aristida congesta</i> subsp. <i>barbicollis</i>				1			1	2	3	2	3	2					
<i>Neuracanthus africanus</i>					1		1	2	4	1	1	2					
<i>Barleria lancifolia</i>					1		1	2	2	2		1					
<i>Eragrostis rigidior</i>		1		1	1		1	1		2	2	1					

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE						DIABASE	HYGRO- PHILOUS			
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Eragrostis superba</i>							1	1	1	2	4	1					
<i>Combretum hereroense</i>					1			1	1	1	1		3		2		1
<i>Dicoma tomentosa</i>							1	1	1		1	1					
<i>Dalechampia galpinii</i>									1	2							
<i>Aptosimum lineare</i>								1	2								
<i>Sterculia rogersii</i>					1				1	2		1					
Q <i>Combretum apiculatum</i>	2	2	5	4	5	1	1	1	5	4	2	5					
<i>Aristida congesta</i> subsp. <i>con-</i> <i>gesta</i>	1	2	3	3	2	2	3	4	5	5	3	3					
<i>Indigofera vicioides</i>	1	3	1	1	1	1	1	2	3	4	2	2	2				
<i>Cissus lonicerifolius</i>	1	2	2	2	1	1	1	1	3	1	2	2					
<i>Hermannia glanduligera</i>	3	2	1	3	2	1	1	1	1	1	2	1	3				
<i>Rhynchosia totta</i>	3	1	2		1	1	1	1	3	3	2	2	3				
<i>Phyllanthus burchellii</i>	1	5	3	1	1	3		1	3		1	2	2				
<i>Hibiscus engleri</i>	2	2	2	2	2	2	2	1		1	1	1			2		
<i>Brachiaria nigropedata</i>	2	3	1	3	1	1			1	1	2	2					
<i>Vigna unguiculata</i>	3	2	4	4	1	1	1	1			2	2					
<i>Commelina africana</i>	2		2	1	1	1	2	1			1	1					
<i>Acalypha indica</i>	1	1	2	1	1	1	2	1	2	2	1	1	2				
<i>Boscia albitrunca</i>	1	1	2	3	2	1	1	1	1			2					
<i>Commelina erecta</i>	2	3	1	2	2	1	2	1	1								
<i>Monechma monechmoides</i>		1	3	2	1	2	1	1	3		1	1					
<i>Enneapogon cenchroides</i>	1		1	3	2	1	3	4	5	2	2	2					
<i>Phyllanthus pentandrus</i>	1		1	1	1	1	1	2	1	4	1	3					
<i>Tephrosia polystachya</i>	1	2	5	3	1	1		1	3	3	2	3					
<i>Cassia abbreviata</i>	1	1	1		1	1			1		1	1					
<i>Schmidtia pappophoroides</i>	2	2	4	4	1			2	2		3	4					
<i>Hibiscus sidiformis</i>		1	1	1	1	2	1	1	2			2					
<i>Kyphocarpa angustifolia</i>	1	1	1	1	3				1	2	1						
<i>Grewia bicolor</i>	1		2	2	2	1	3	4	4	4	2	3	2				
<i>Dalbergia melanoxylon</i>	2		4	3	1		1	1	1	4	3	2					
<i>Pseudobrachiaria deflexa</i>		2			1	3	2	1	3		1	1					
<i>Pupalia lappacea</i>	1			2	2	3	3	1	2				2				
<i>Evolvulus alsinoides</i>	1	1	1	2	2	1		1	3	2		1					
<i>Tragus berteronianus</i>			1	1	1		3	1	1	1	1	1					
<i>Cassia mimosoides</i>	1			2		1		1			2	1					
<i>Euphorbia polycnemoides</i>	1			1	3	1		1	3	2	1	2					
<i>Crotalaria virgulata</i>		1	1	1		1		2	1								
<i>Euphorbia tettensis</i>	2		3	2				1	3	1	1	2					
<i>Maytenus heterophylla</i>			1		1		1	1	1	1	4	1					
<i>Cucumis anguria</i>				2		1	1	1	1		1						
<i>Corchorus asplenifolius</i>	1			3		1	1		2	2	1						
<i>Lantana rugosa</i>	2		1		1	1			1		2						
<i>Tricalysia allenii</i>	1	1		1	2				1		1						

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPERMUM MOPANE					DIABASE	HYGROPHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2	3	4	1.1	1.2	1.3	1.4
<i>Ipomoea obscura</i>				1		1	2	1	1		1	1					
<i>Grewia monticola</i>			3	1	1	1		1			1	1					
<i>Mundulea sericea</i>	1		1	1	1				1		1	1					
<i>Cymbopogon excavatus</i>				1					1	1	2	1	3	2			
<i>Markhamia acuminata</i>				2	1				1		1	1					
<i>Gardenia resiniflua</i>			1	1	1	1	1	1	1								
<i>Justicia protracta</i>	1							1	1								
<i>Barleria affinis</i>					1				1								
<i>Stylochiton natalensis</i>	1				1	1		1									
<i>Eragrostis curvula</i>				1								1					
<i>Ipomoea pes-tigrides</i>	1	2		1			1	1									
<i>Zornia diphylla</i>	1	2		1	1				1			1					
<i>Clerodendron ternatum</i>	1		1	1				1	1	1	1	1					
<i>Justicia flava</i>					1		1	1				1					
<i>Manilkara moehria</i>	1			1	1			1									
<i>Rhynchosia minima</i>	1							1			1	1					
<i>Eragrostis heteromera</i>				1			1		1								
<i>Grewia hexamita</i>		1	1	1	1	1			1		1		2				
<i>Gisekia africana</i>				1			2				1						
<i>Commiphora edulis</i>					1	1			1								
<i>Anisotes sessiliflorus</i>		1			1		1	1	1								
<i>Cardiospermum haliacabum</i>					1			1									
<i>Aspilia mossambicensis</i>	1								1			1					
<i>Dactyloctenium aegyptium</i>				1			1										
<i>Polygala wilmsii</i>	2		1		1				1		1						
<i>Calostephane divaricatum</i>				1	1			1	1								
<i>Hermboetia odorata</i>	1							1		1		1					
<i>Kyllinga alba</i>	1					1		1			1	1					
<i>Kohautia virgata</i>	2						1	1		1		1					
<i>Gardenia spatulifolia</i>			1	1		1											
<i>Cissus quadrangularis</i>					1	1	1	1									
<i>Stipagrostis uniplumis</i>	1			1				1		1							
<i>Eragrostis lehmanniana</i>				1			1	1									
<i>Leptactinia benguelensis</i>		1	1		1	1		1									
<i>Ipomoea crassipes</i>											1						
<i>Orthosiphon suffrutescens</i>								1	1								
<i>Grewia villosa</i>					1	1	1		1		1						
<i>Lippia javanica</i>								1	1		1		2				
<i>Merremia palmata</i>											1	1					
<i>Endostemon tenuiflorus</i>									1	1							
R <i>Setaria holstii</i>													4	3	2		
<i>Piliostigma thonningii</i>													3				
<i>Hyparrhenia rufa</i>													3				
<i>Helichrysum miconiifolium</i>													3				

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPERM MOPANE					DIABASE	HYGROPHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2		3	4	1.1	1.2	1.3
<i>Ipomoea papilio</i>						1							3				
<i>Acacia gerrardii</i>											1		2				
S <i>Acacia borleae</i>														5			
<i>Tetrapogon mossambicensis</i> ..								1						5			
<i>Cephalocroton mollis</i>											1			5			
<i>Ruellia patula</i>				1			1	1	1		1	1		5			
<i>Brachiaria erucaeformis</i>														3			
T <i>Sesbania sesban</i>															4		
<i>Fuirena pubescens</i>															3		
U <i>Acacia albida</i>																5	
<i>Ficus sycomorus</i>																4	
<i>Acacia robusta</i>																4	
<i>Trichilia emetica</i>																4	
<i>Diospyros mespiliformis</i>																4	
<i>Hypoestes verticillaris</i>																3	
<i>Abutilon angulatum</i>																3	
<i>Tabernaemontana elegans</i>	1				1											3	
V <i>Setaria sphacelata</i>									1			1	2	3	3		3
<i>Ischaemum afrum</i>														5	4		2
<i>Ischaemum brachyatherum</i> ...														3	2		1
<i>Panicum meyerianum</i>															4	3	4
<i>Echinochloa pyramidalis</i>															3	2	2
<i>Acacia xanthophloea</i>																3	1
<i>Sporobolus consimilis</i>																2	2
<i>Xanthocercis zambesiaca</i>																3	1
<i>Kigelia africana</i>																2	1
<i>Cyperus fenzelianus</i>																	2
<i>Croton megalobotrys</i>																	1
<i>Chloris gayana</i>	1																1
W <i>Panicum maximum</i>	4	5	5	5	4	3	5	4	4	1	3	4	2		4	5	3
<i>Digitaria eriantha</i>	5	4	5	5	5	2	1	3	4	4	5	5	2	3	3	4	
<i>Hibiscus micranthus</i>	1	1	2	2	3	3	3	4	5	3	1	4			2		
<i>Lonchocarpus capassa</i>	1	1		3	1	1	1	1			2		3		4	4	2
<i>Spirostachys africana</i>	1	3	1	1	1		1	2							4		1
<i>Combretum imberbe</i>					1		1	1	1	1	3	1	2		3	3	2
<i>Solanum panduraeforme</i>	2				2	2	1	2	2	1	2	3			2		1
<i>Dichrostachys cinerea</i>	2	3	1	3	2	1	1	1	2	2	2	3	4		2		1
<i>Combretum mossambicensis</i> ..	1	2	2	3	1	1	1	1	2	1		2	2				1
<i>Acacia nigrescens</i>	1				2		2	3	3	4	2	4	3		4		
<i>Securinega virosa</i>		2	1	1	1		1	1	1		1	1		5			1

PLANT SPECIES	COMMUNITIES																
	SANDVELD						COLOPHOSPER- MUM MOPANE					DIABASE	HYGRO- PHILOUS				
	1.1	1.2	1.3	1.4	2.1	2.2	1.1	1.2	1.3	2.1	2.2		3	4	1.1	1.2	1.3
<i>Vernonia fastigiata</i>	4			1	2	2	1	1	2	1	3	1		5			
<i>Cenchrus ciliaris</i>			1					1	2		2	1					1
<i>Achyranthes aspera</i>	1			1	1	3	1	1	1							5	1
<i>Indigofera rhytidocarpa</i>	1	1		2			3	1	1	2	1	1					
<i>Lannea stuhlmannii</i>		2	1	1			1	1	1		1	1			2		
<i>Leucas glabrata</i>	1		1	2	1	1	1	1	2								1
<i>Melhania forbesii</i>	1	1	3	2	1			2	1	1	1	2					1
<i>Monechma divaricatum</i>			1	2			1	1									
<i>Sclerocarya caffra</i>	1	1	2	1	1				1	1	1	1			2		
<i>Rhynchelytrum villosum</i>			1	2	1	2		1	2	3	1	1	2				
<i>Commiphora mollis</i>				2				1	2	2		1					
<i>Becium obovatum</i>				1		1	1	1	3			1					
<i>Asparagus setaceus</i>	1			1	1	2	2	1	1	1		1		3			
<i>Corchorus kirkii</i>		2	2	1	1			1	1		1	1			3		1
<i>Tragia rupestris</i>	1		1	1	1		1	1			1	2			2		1
<i>Grewia flavescens</i>		2		1	1	1		1								2	
<i>Maytenus senegalensis</i>				1									2				1
<i>Leonotis nepetifolia</i>	2			1	1	1							2				1
<i>Pterocarpus rotundifolius</i>											1		2				
<i>Ceratotheca triloba</i>				1			1		1		1				2		
<i>Barleria transvaalensis</i>							1	1	1								
<i>Peltophorum africanum</i>	2				1			1					2				
<i>Hemizygia bracteosa</i>	1	1	2	1	1					1		1			2		
<i>Albizia harveyi</i>									1		1	1			2		
<i>Abutilon guineense</i>				1	1		1	1	1					2			1
<i>Ziziphus mucronata</i>				1	1		1	1		1		1					1
<i>Melhania rehmannii</i>					1	1		1			1						1
<i>Cyperus</i> sp.					1		1	1		1					2		
<i>Ormocarpum trichocarpum</i> ...								1			1		2		2		
<i>Abutilon ramosum</i>							1				1		2				1
<i>Indigofera schimperi</i>	1				1						1	1		3	2		
<i>Cassia petersiana</i>	1	1	1	1							1		2				

tree savanna and the *Colophospermum mopane*-*Themeda triandra* shrub savanna change gradually into the *Colophospermum mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna to the north. In general all the *Colophospermum mopane* communities are characterised by the following habitat factors: shallow to moderately deep sandy clay loam to clay soils; neutral pH; presence of carbonates; soils that have a normal soluble salt concentration to soils that are fairly leached. The communities occur on alluvium, shale, basalt, andesite and the Malvernian Formation on plains or undulating country.

1. The *Colophospermum mopane*–*Euclea divinorum* tree savanna

This savanna is found on alluvial soils and basalt hills in the Pafuri area as well as on shale in the Punda Milia area. It is subdivided into three communities (1.1, 1.2, 1.3) (Table 1). The *Colophospermum mopane*–*Acacia tortilis*–*Urochloa mosambicensis* tree savanna (1.1) is characterised by species group I; the *Colophospermum mopane*–*Euclea divinorum*–*Enteropogon macrostachyus* tall tree savanna (1.2) by species group J and the *Colophospermum mopane*–*Commiphora glandulosa*–*Seddera capensis* open tree savanna (1.3) by species group K, while the relationships between these three communities and the other *Colophospermum mopane* communities is indicated by the mutual presence of species group P.

According to Werger and Coetzee (1977) *Euclea divinorum* together with *Enteropogon macrostachyus*, *Achyranthes* spp., *Chloris virgata* and *Dactyloctenium aegyptium* can be regarded as differential species of the brackish plains in the Transvaal Lowveld. *Adansonia digitata* is strongly associated with the *Colophospermum mopane*–*Commiphora glandulosa*–*Seddera capensis* open tree savanna (1.3) and forms a prominent feature along the Nyala Drive and in the Mukahandja area (Fig. 5).

The major difference between the habitat of these three communities lies in the geological substrate on which they are found. Community 1.1, 1.2 and 1.3 are found on alluvial plains, shale and basalt respectively. Community 1.3 is also characterised by a shallow, rocky soil with high carbonate concentrations.

1.1 The *Colophospermum mopane*–*Acacia tortilis*–*Urochloa mosambicensis* tree savanna

This community is found along the Levubu River in the Pafuri area and in the vicinity of Punda Milia where it occurs along the Madzaringwe stream as well as the Levubu River. It usually occurs on alluvial flood plains between 200 and 460 m above sea level (Figs 1 & 2).

The fine to medium textured sandy clay loam to clay soils vary from brown to brownish black. Up to five per cent of the soil surface is covered by stones and usually the soil is deeper than 1 m. The topsoil has a moderately developed blocky structure with a friable to firm consistency and a pH ranging from 6.0 to 8.8. Carbonates are often present.

Floristic composition

Trees grow up to 8 m high with *Acacia tortilis* being the most conspicuous species especially in the Pafuri area. Shrubs and sparse shrubs, usually reaching 2 m in height, include species such as *Maerua parvifolia*, *Grewia bicolor* and *Azima tetracantha*. Species favouring the brackish plains along the Levubu River are *Acacia senegal* var. *rostrata*. Associated species within this community are

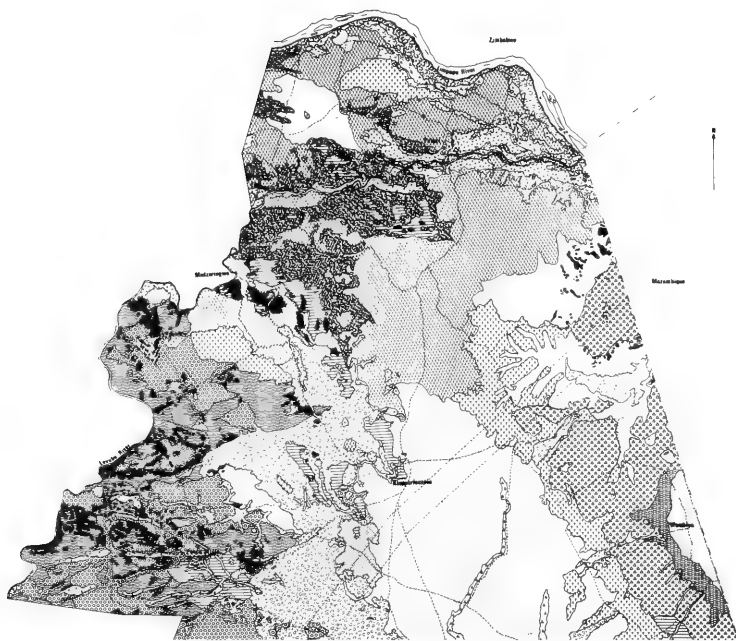


FIG. 1.

Vegetation map of the Punda Milia-Pafuri-Wambya area in the Kruger National Park.

Commiphora glandulosa, *Ximenia americana*, *Thilachium africanum*, *Gardenia resiniflua*, *Maytenus heterophylla* and *Dalbergia melanoxylon*.

In certain areas the herbaceous component is poorly developed. Sporadic flooding as well as intense grazing and browsing in these areas lead to an abundance of pioneer species such as *Alternanthera pungens*, *Trianthema triquetra*, *Cyathula crispula*, *Corbichonia decumbens*, *Pupalia lappacea*, *Tragus berteronianus* and *Aristida congesta* subsp. *congesta*. However, in a favourable rainy season a good grass cover of *Urochloa mosambicensis* and *Panicum maximum* is formed, together with species such as *Chloris virgata*, *Sporobolus smutsii*, *Enneapogon cenchroides* and *Hibiscus micranthus*. A number of widespread herbaceous species within this community are *Chloris roxburghiana*, *Setaria verticillata*, *Urochloa trichopus*, *Mollugo nudicaulis*, *Epaltes gariepina*, *Acanthospermum hispidum*, *Dactyloctenium aegyptium*, *Justicia protracta* and *Pseudo-brachiaria deflexa*.



FIG. 2.

The *Colophospermum mopane*-*Acacia tortilis*-*Urochloa mosambicensis* tree savanna on alluvial soil along the Levubu River.

Termitaria occur throughout this community and an entire termitarium is often covered by *Capparis tomentosa* which grows in the form of a dense bush. According to Wild (1952) members of the family Capparaceae are frequently found on termitaria in southern Zimbabwe.

In Figure 1 this tree savanna is subdivided into 3 communities namely the *Acacia tortilis* tree savanna, the *Acacia senegal* shrub savanna and the *Salvadora angustifolia* shrub savanna.

Structure

The structural analysis of the woody component of this community is given in Tables 2 and 3 as well as in Figures 10 and 11.

A high total percentage canopy spread is found in the 1 m and 2 m strata while the higher strata, e.g. the > 6 m stratum is relatively poorly developed (Table 2). *Colophospermum mopane* and *Acacia tortilis* (Table 3) are species that contribute significantly to the canopy spread in the 1 m and 2 m strata. In the 0.5 m stratum *Colophospermum mopane*, *Acacia tortilis* and *Maerua parvifolia* have high canopy spread percentages. Species of the 3 m height class have

TABLE 2.

Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv./ha) in different height classes of woody plant species in the *Colophospermum mopane*-*Acacia tortilis*-*Urochloa mosambicensis* tree savanna.

		Percentage canopy spread										Mean number of indiv./ha			
Stratum (m)	Total*	Growth form			Height class						Height class (m)	Total	Growth form		
		Tree	Sparse shrub	Shrub	> 6m	4-5m	3 m	2 m	1 m	0,5 m			Tree	Sparse shrub	
> 6	2,23	1,91	0,22	0,10	2,23	2,29	2,95				> 6	17	16	1	
4-5	5,24	2,77	1,69	0,78	2,29	3,62	2,95				4-5	53	18	27	
3	8,61	2,86	3,80	1,95	1,54	3,62	3,45				3	206	28	122	
2	12,33	2,64	6,30	3,39	1,12	2,93	5,06	3,22			2	250	53	126	
1	11,71	1,93	6,37	3,41	0,74	1,64	3,77	3,32	2,24		1	354	32	203	
0,5	8,07	0,69	4,24	3,14	0,22	0,71	1,93	1,92	2,14	1,15	0,5	323	61	183	
											Total	1 203	208	662	
															333

*Figures in this column are referred to in the text as "Total percentage canopy spread" values

TABLE 3.
Percentage canopy spread in different strata; mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*-*Acacia tortilis*-*Urochloa mosambicensis* tree savanna.

Plant species*	p.a.c.	Indiv./ha	Percentage canopy spread					
			Stratum (m)					
			> 6	4-5	3	2	1	0,5
<i>Colophospermum mopane</i>	8,29	369	1,21	1,91	3,34	5,23	5,01	3,30
<i>Acacia tortilis</i>	5,64	158	0,88	2,42	3,44	3,77	2,43	0,91
<i>Maerua parvifolia</i>	1,03	87				0,08	0,77	0,92
<i>Balanites pedicularis</i>	0,92	50			0,21	0,87	0,59	0,06
<i>Salvadora angustifolia</i>	0,81	73			0,21	0,67	0,54	0,48
<i>Anisotes sessiliflorus</i>	0,70	70					0,21	0,68
<i>Acacia senegal</i> var. <i>rostrata</i>	0,64	32		0,29	0,47	0,44	0,21	0,14
<i>Acacia grandicornuta</i>	0,63	8	0,10	0,43	0,55	0,56	0,42	0,21
<i>Grewia bicolor</i>	0,60	35			0,02	0,09	0,58	0,38
<i>Azima tetracantha</i>	0,56	161					0,38	0,47

* Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

the highest total percentage canopy spread in the 2 m stratum (5,06 %). The 0,5 m and 1 m height classes, where shrubs and sparse shrubs are most numerous, have the highest densities (Table 2).

Species with the highest percentage apparent canopy cover (p.a.c.) and densities are *Colophospermum mopane* (8,29 % and 369 indiv/ha), *Acacia tortilis* (5,64 % and 158 indiv/ha) and *Maerua parvifolia* (1,03 % and 87 indiv/ha) (Table 3). *Azima tetracantha* has a low percentage apparent canopy cover but a high density.

1.2 The *Colophospermum mopane*-*Euclea divinorum*-*Enteropogon macrostachyus* tall tree savanna

This community is usually found on shale at 215 to 460 m above sea level on plains as well as on gentle slopes with a gradient up to 8° (Figs 1 & 3).

The dark brown to brownish black, fine to medium textured loamy sand to clay soils range from 70 mm to more than 1 m deep. Up to 20 % of the soil surface is covered by stones. The topsoil has a moderate blocky structure, a friable consistency and a pH between 6,1 and 8,7. The soils have a moderate salt concentration or are sometimes strongly leached. Carbonates are present in most cases.



FIG. 3.

The *Colophospermum mopane*-*Euclea divinorum*-*Enteropogon macrostachyus* tall tree savanna on shale of the Karroo System.

Floristic composition

Trees, mainly *Colophospermum mopane*, *Acacia nigrescens* and *Spirostachys africana*, grow up to 15 m tall. The tallest individuals are found in areas with a deep sandy clay loam. This coincides with the findings of Thompson (1960) that *Colophospermum mopane* will grow better on fertile, slightly acid, friable, permeable soils. The shrub and sparse shrub strata are well developed up to 3 m and are characterised by species such as *Euclea divinorum*, *Grewia bicolor* and *Ximenia americana*. The associated species in this community are *Maerua parvifolia*, *Zanthoxylum capense*, *Thilachium africanum*, *Acacia grandicornuta*, *Combretum imberbe*, *Dichrostachys cinerea* and *Combretum hereroense*.

The herbaceous component consists mainly of *Enteropogon macrostachyus*, *Enneapogon cenchroides*, *Chloris roxburghiana*, *Amaranthus thunbergii*, *Panicum maximum* and *Hibiscus micranthus*. While *Enneapogon cenchroides* is found mainly on relatively shallow rocky soils, *Enteropogon macrostachyus* favours deeper soils. Other common herbaceous species within this tall tree savanna are *Aristida congesta* subsp. *congesta*, *Digitaria eriantha*, *Tetrapogon tenellus*, *Seddera capensis*, *Elytrarea acaulis*, *Abutilon fruticosum*, *Ecbolium revolutum*, *Bothriochloa insculpta*, *Crotalaria virgulata* and *Indigofera vicioides*.

Terminalia prunioides and *Commiphora* spp. only occur north of Xantangelane in this community.

Structure

The structural analysis of the woody component of the tall tree savanna is given in Tables 4 and 5 as well as in Figures 10 and 11.

In general a relatively high total percentage canopy spread is found from the 0.5 m to the 4–5 m stratum, with the highest percentage in the 2 m stratum (Table 4). Species contributing substantially to the canopy spread in this stratum are *Colophospermum mopane*, *Euclea divinorum*, *Gardenia resiniflua* and *Terminalia prunioides* (Table 5). In the >6 m stratum *Colophospermum mopane* and *Spirostachys africana* are the important species. Shrubs have the highest total percentage canopy spread in the 0.5 m and 1 m strata, sparse shrubs in the 2 m and 3 m strata and trees in the 4–5 m and >6 m strata. The largest mean number of individuals occur in the 0.5 m and 1 m height classes where shrubs and sparse shrubs are the most numerous of the various growth forms while the sparse shrubs collectively have the highest density. The relatively high density in the >6 m height class is apparent from Table 4. Many of these trees reach 15 m in height. *Colophospermum mopane* and *Euclea divinorum* are physiognomically the most conspicuous species and have the highest densities and percentage apparent canopy cover.

1.3 The *Colophospermum mopane*–*Commiphora glandulosa*–*Seddera capensis* open tree savanna

This open tree savanna lies in the northern part of the study area, between

TABLE 5.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*-*Euclea divinorum*-*Enteropogon macrostachyus* tall tree savanna.

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread				
			Stratum (m)				
			> 6	4-5	3	2	1
<i>Colophospermum mopane</i>	19,02	1 322	4,83	6,36	7,35	9,11	8,63
<i>Euclea divinorum</i>	2,50	162			0,25	1,97	1,76
<i>Spirostachys africana</i>	2,42	49	0,71	2,03	1,58	0,52	0,10
<i>Grewia bicolor</i>	1,39	108			0,01	0,66	1,12
<i>Terminalia prunioides</i>	1,35	34	0,14	0,60	1,00	0,75	0,46
<i>Combretum apiculatum</i>	1,25	59	0,02	0,54	0,90	0,71	0,43
<i>Gardenia resiniflua</i>	0,94	19			0,42	0,89	0,75
<i>Acacia grandicornuta</i>	0,86	42		0,11	0,52	0,65	0,40
<i>Anisotes sessiliflorus</i>	0,73	100					0,47
<i>Securinega virosa</i>	0,63	45				0,27	0,53

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

215 and 415 m above sea level. It occurs mainly on basalt, on plains as well as on moderate to steep slopes with a gradient up to 12° (Figs 1, 4 & 5).

The basalt, andesite and shale, underlying this savanna, weathers to a fine textured brownish black sandy clay loam to clay soil. The soils are from 30 mm to 600 mm deep and up to 40 % of the surface is covered with stones and rocks. The topsoil is apedal with a moderately to well developed blocky structure and a loose to friable consistency. The soil is neutral to alkaline and has a normal to moderate soluble salt concentration. Carbonates are usually present in high concentrations.



FIG. 4.

The *Colophospermum mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna on basalt in the Pafuri area.

Floristic composition

The physiognomically striking species, *Colophospermum mopane*, *Kirkia acuminata*, *Sclerocarya caffra* and *Adansonia digitata*, are 6 to 10 m high. The smaller trees and sparse shrubs such as *Combretum apiculatum* and *Commiphora glandulosa*, reach a height of 6 m, while shrubs such as *Grewia bicolor*, *Terminalia prunioides* and *Cissus lonicerifolius* are up to 2 m tall. Other widespread species include *Acacia nigrescens*, *Maerua parvifolia*, *Zanthoxylum capense*,

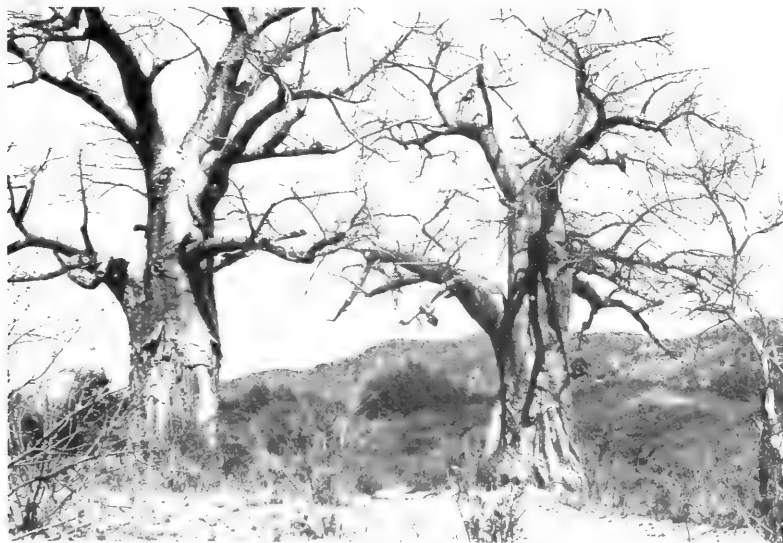


FIG. 5.

Adansonia digitata, one of the most conspicuous trees in the *Colophospermum mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna.

Commiphora mollis, *C. edulis*, *Sterculia rogersii*, *Markhamia acuminata*, *Gardenia resiniflua*, *Grewia villosa*, *Dichrostachys cinerea* and *Combretum mossambicense*. Whereas *Euclea divinorum*, *Spirostachys africana* and *Lonchocarpus capassa* are abundant in the previously described tall tree savanna they are almost absent in this open tree savanna.

The herbaceous component is characterised by the presence of *Enneapogon cenchroides*, *Aristida congesta* subsp. *congesta*, *Hibiscus micranthus*, *Neuracanthus africanus*, *Panicum maximum* and *Digitaria eriantha*. Other associated herbaceous species are *Aristida congesta* subsp. *barbicollis*, *Evolvulus alsinoides*, *Rhynchosia totta*, *Euphorbia tettensis*, *Seddera capensis*, *Fingerhuthia africana*, *Bothriochloa insculpta*, *Ecbolium revolutum*, *Indigofera vicioides*, *Monechma monechmoides*, *Tephrosia polystachya* and *Dalechampia galpinii*.

Structure

The structural analysis of this open tree savanna is given in Tables 6 and 7 as well as in Figures 10 and 11.

The highest total percentage canopy spread is found in the 2 m stratum (Table 6) where *Combretum apiculatum*, *Colophospermum mopane* and *Grewia*

TABLE 6.

Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv./ha) in different height classes of woody plant species in the *Colophospermum mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna.

Stratum (m)	Percentage canopy spread										Mean number of indiv./ha		
	Total*	Growth form			Height class					Height class (m)	Total	Growth form	
		Tree	Sparse shrub	Shrub	> 6m	4-5m	3 m	2 m	1 m	0,5 m		Tree	Sparse shrub
> 6	5,87	5,31	0,56		5,87	4,50				> 6	55	51	4
4-5	9,60	7,04	1,99	0,57	5,10	4,50				4-5	132	74	43
3	12,32	5,25	3,57	3,50	2,47	4,50	5,35			3	241	84	102
2	16,01	3,52	6,25	6,22	1,36	3,00	6,73	4,90		2	392	77	183
1	13,02	1,90	5,51	5,61	0,32	1,33	3,62	4,62	3,13	1	448	54	256
0,5	8,99	0,78	3,49	4,72	0,09	0,44	1,28	2,93	2,75	0,5	457	62	297
										Total	1 725	402	885
													438

*Figures in this column are referred to in the text as "Total percentage canopy spread" values

TABLE 7.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*–*Commiphora glandulosa*–*Seddera capensis* open tree savanna.

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
Colophospermum mopane	16,20	994	4,41	6,42	5,46	5,92	5,83	4,38
Combretum apiculatum	8,42	241	0,07	1,22	4,82	6,67	3,58	1,38
Grewia bicolor	1,80	87			0,09	0,97	1,35	1,02
Acacia nigrescens	1,10	30	0,52	0,80	0,63	0,59	0,36	0,21
Terminalia prunioides	0,52	14	0,02	0,15	0,37	0,35	0,21	0,05
Commiphora glandulosa	0,50	24		0,40	0,19	0,16	0,08	0,07
Maerua parvifolia	0,35	72	0,18			0,02	0,18	0,19
Cissus lonicerifolius	0,29	18			0,04	0,15	0,19	0,15
Mundulea sericea	0,23	7			0,03	0,23	0,09	
Zanthoxylum capense	0,20	17				0,02	0,19	0,13

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

bicolor contribute more than the other species to the high value. Shrubs and sparse shrubs have high total percentage canopy spread values in the lower strata (up to 2 m) whereas trees have the highest percentage in the 3 m and higher strata (Table 7). In the >6 m stratum *Colophospermum mopane*, *Acacia nigrescens* and *Commiphora glandulosa* have high canopy spread percentages.

Individuals of the 0.5 m, 1 m and 2 m height classes, where sparse shrubs are most numerous, occur in high densities. Although sparse shrubs have the highest densities up to the 3 m stratum, they do not contribute the most to the total percentage canopy spread in those strata. Species with high percentage apparent canopy cover values and densities are *Colophospermum mopane*, *Combretum apiculatum* and *Grewia bicolor* (Table 6).

2. The *Colophospermum mopane*-*Dalbergia melanoxylon*-*Heteropogon contortus* shrub savanna

This savanna covers the whole southern part of the central basalt plains as well as large areas of the Malvernian Formation on the eastern and western border of the Pafuri area. It can be divided into two communities (2.1, 2.2) which are characterised by species groups L and N respectively (Table 1), while species groups M, O and P reveal the affinities with the other *Colophospermum mopane* communities. The absence of species such as *Euclea divinorum*, *Boscia albitrunca*, *Sterculia rogersii*, *Spirostachys africana*, *Acalypha indica*, *Pupalia lappacea*, *Pseudobrachiaria deflexa* and *Hibiscus sidiiformis* in community 2.2 is noteworthy.

Community 2.1 is found on the Malvernian formation on dark brown soil with a high pH and high carbonate concentration while community 2.2 is found on basalt and andesite on a dark red brown to brownish black soil with a neutral pH and no carbonates.

2.1 The *Colophospermum mopane*-*Enneapogon scoparius* shrub savanna

This shrub savanna is found at 215 to 445 m above sea level on moderate slopes with a gradient from 2° to 10°. The community appears in two isolated patches, one along the Shilahladonga and the other at Matule Hill in the Pafuri area (Figs 1, 6 & 7).

The parent material weathers to a shallow, fine textured dark brown sandy loam, sandy clay loam or clay soil. Up to 10 % of the soil surface is covered with stones. The topsoil has a poorly developed blocky structure and a friable consistency. The soil is alkaline with a pH ranging from 7.9 to 8.4 and has a normal to moderate soluble salt concentration. Carbonates are present in high concentrations.

According to the physiognomic classification of Tinley (1969) the community at Shilahladonga should be classified as a shrub savanna whereas the variation at Matule Hill should be described as a tree savanna. Both variations are characterised by species group L (Table 1) but they differ structurally.

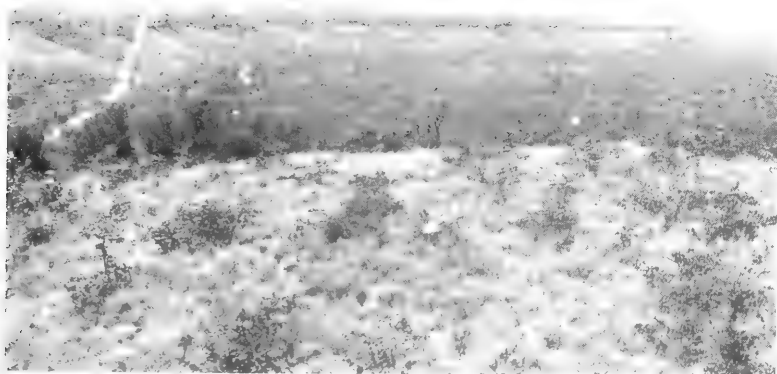


FIG. 6.

The Shilahlandonga variation of the *Colophospermum mopane*–*Enneapogon scoparius* shrub savanna in the foreground.

Floristic composition

The community is characterised by the presence of *Colophospermum mopane*, *Maytenus heterophylla*, *Euclea schimperi* and *Dalbergia melanoxylon*. At Shilahlandonga trees do not normally become more than 5 m high, whereas they grow up to 8 m high at Matule. Shrubs reach up to 2 m and include species such as *Grewia bicolor*, *Maytenus heterophylla* and *Acacia nigrescens* as well as *Combretum apiculatum*, *Terminalia prunioides*, *Euclea divinorum*, *Sterculia rogersii* and *Commiphora mollis*.

The herbaceous component is characterised by *Enneapogon scoparius*, *Seddera capensis*, *Aristida congesta* subsp. *congesta* with associated species including *Heteropogon contortus*, *Fingerhuthia africana*, *Indigofera vicioides*, *Rhynchosia totta*, *Eragrostis superba*, *Barleria lancifolia*, *Tephrosia polystachya* and *Phyllanthus pentandrus*. The absence of *Panicum maximum* is noteworthy.

Isolated patches of the *Androstachys johnsonii*–*Croton pseudopulchellus* dry forest often occur within this community on south and north facing slopes. In the "kloofs" within this community a number of other species are found such as



FIG. 7.

The Mature variation of the *Colophospermum mopane*-*Enneapogon scoparius* shrub savanna.

Kirkia acuminata, *Ptaeroxylon obliquum*, *Maerua angolensis*, *Commiphora tenuipetiolata*, *Albizia brevifolia*, *Adansonia digitata*, *Strychnos decussata* and *Pappea capensis*.

Structure

The structural analysis of the woody component of this community is given in Tables 8, 9, 10 and 11 as well as in Figures 10 and 11. Since the structure of the two isolated patches differ, the variations are discussed separately.

a. The Shilahlandonga variation (Tables 8 and 9 and Fig. 6)

The highest total percentage canopy spread is found in the 0,5 m stratum. Shrubs have the highest values in the 0,5 m and 1 m strata although sparse shrubs are more numerous in the 0,5 m stratum. From the 2 m stratum and above, the total percentage canopy spread is low (Table 8). *Colophospermum mopane* has high canopy spread percentages in all the strata up to the 4-5 m stratum with the exception of the 3 m stratum. *Terminalia prunioides* also has a high percentage canopy spread in the 2 m and 3 m strata (Table 9). The sparse shrubs have the highest density of the three growth forms and no plants are found in the >6 m stratum. Species with a high percentage apparent canopy cover are *Colophospermum mopane* and *Terminalia prunioides*.

TABLE 8.

Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv./ha) in different height classes of woody plant species in the *Colophospermum mopane*–*Emmenanthe scapariis* shrub savanna (Shilahladonga variation).

Stratum (m)	Percentage canopy spread								Mean number of indiv./ha				
	Total*	Growth form			Height class				Height class (m)	Total	Growth form		
		Tree	Sparse shrub	Shrub	>6 m	4-5 m	3 m	2 m			1 m	0,5 m	Tree
>6	0,10	0,10			0,10				>6	2	2		
4-5	1,74	0,60	0,81		0,05	1,69			4-5	66	41	9	16
3	2,97	1,02	1,40		0,01	1,67	1,29		3	150	94	36	20
2	7,20	1,00	4,42			0,90	0,88	5,42	2	933	66	433	434
1	9,01	0,20	5,60			0,12	0,24	4,36	1	1 666		1 100	566
0,5								4,29	0,5				
									Total	2 817	203	1 578	1 036

*Figures in this column are referred to in the text as "Total percentage canopy spread" values

TABLE 9.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*-*Enneapogon scoparius* shrub savanna (Shilahladonga variation).

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread					
			>6	4-5	Stratum (m)			
					3	2	1	0,5
<i>Colophospermum mopane</i>	8,99	1 759		0,10	0,68	1,38	5,44	5,93
<i>Terminalia prunioides</i>	1,08	22			0,98	1,04	0,52	0,10
<i>Euclea schimperi</i>	0,85	100					0,17	0,73
<i>Combretum apiculatum</i>	0,55	201			0,02	0,06	0,08	0,49
<i>Dalbergia melanoxylon</i>	0,49	242				0,07	0,22	0,41
<i>Sterculia rogersii</i>	0,29	8				0,29	0,19	0,04
<i>Cissus lonicerifolius</i>	0,26	33					0,26	0,09
<i>Strychnos madagascariensis</i>	0,20	50					0,15	0,10
<i>Acacia nigrescens</i>	0,04	1			0,02	0,04	0,01	
<i>Commiphora mollis</i>	0,04	1			0,04	0,02		

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

b. The Matule variation (Tables 10 and 11 and Fig. 7)

In contrast to the previous variation, the highest total percentage canopy spread occurs in the >6 m stratum, where trees and sparse shrubs have high percentages (Table 10). *Colophospermum mopane* has the highest percentage canopy spread in all the strata save the 1 m stratum while *Grewia bicolor* and *Dichrostachys cinerea* also have high values in the 0.5 m and 1 m strata (Table 11). Sparse shrubs collectively are most numerous while shrubs are relatively scarce from the 3 m stratum upwards. *Colophospermum mopane* and *Grewia bicolor* have high apparent canopy cover values while *Colophospermum mopane*, *Dichrostachys cinerea*, *Acacia nigrescens*, *Combretum apiculatum* and *Grewia bicolor* have high densities (Table 11).

2.2 The *Colophospermum mopane*-*Themeda triandra* shrub savanna

This community is found on the plains southeast of Klopperfontein at 385 to 452 m above sea level (Figs 1 & 8).

The basalt and andesite of the Karroo System which occurs in this area weathers to a fine to medium textured dark red brown to brown black sandy clay loam or clay soil varying from 90 to 850 mm in depth. The topsoil has a moderately to well developed blocky structure and a friable to firm consistency. No stones are generally found on the soil surface. The pH ranges from 6.1 to 7.4 and the soils have a moderate to normal soluble salt concentration, although it may be leached in certain areas. Carbonates are usually absent.

Floristic composition

Trees are scarce and usually only from 3 to 5 m high, with only a few individuals becoming more than 6 m high. The most striking species are *Colophospermum mopane*, *Combretum imberbe* and *C. apiculatum*. The shrub layer is very well developed and includes species such as *Dalbergia melanoxylon*, *Cissus lonicrifolius*, *Colophospermum mopane* and *Lonchocarpus capassa*. Patches where *Pterocarpus rotundifolius*, *Dalbergia melanoxylon*, *Dichrostachys cinerea* and *Albizia harveyi* are dominant occur localised. The associated species within this community are *Combretum hereroense*, *Cassia petersiana*, *C. abbreviata*, *Grewia bicolor*, *G. monticola*, *Lannea stuhlmannii*, *Acacia nigrescens* and *Maytenus heterophylla*.

The herbaceous component is well developed and characterised by the presence of *Themeda triandra*, *Neorautanenien amboensis*, *Setaria woodii* and *Panicum coloratum*. A few other species which also have high cover values include *Heteropogon contortus*, *Bothriochloa insculpta*, *Digitaria eriantha* and *Panicum maximum*. The associated herbaceous species are *Eragrostis superba*, *Sorghum versicolor*, *Schmidtia pappophoroides*, *Vernonia fastigiata*, *Aristida congesta* subsp. *barbicollis*, *Indigofera heterotricha*, *Heliotropium strigosum*, *Eragrostis rigidior* and *Cenchrus ciliaris*.

TABLE 11.
Percentage canopy spread in different strata: mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*-*Enneapogon scoparius* shrub savanna (Matule variation).

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
Colophospermum mopane	22,61	676	16,20	12,38	6,73	4,85	2,05	2,26
Grewia bicolor	2,99	112				1,67	3,42	2,09
Dichrostachys cinerea	1,61	172				0,47	0,86	1,67
Combretum apiculatum	1,54	115		0,06	1,00	0,87	0,45	0,34
Sterculia rogersii	1,01	6		0,32	0,88	0,83	0,12	
Commiphora mollis	0,73	6	0,25	0,73	0,40	0,05		
Acacia nigrescens	0,70	118		0,06	0,08	0,15	0,28	0,55
Euclea divinorum	0,47	13				0,40	0,47	0,12
Commiphora edulis	0,40	3		0,11	0,30			
Kirkia acuminata	0,35	3		0,35	0,16	0,40		

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)



FIG. 8.

The *Colophospermum mopane*-*Themeda triandra* shrub savanna on the basalt south of Klopfontein.

Dambo's and rain pans occur along streams and on the plains within this community. These areas are characterised by the following species:

Hyphaena natalensis	Sporobolus consimilis
Phoenix reclinata	Sesbania sesban
Combretum imberbe	Setaria sphacelata
Lonchocarpus capassa	Ischaemum afrum

Structure

The structural analysis of the woody component of this community is given in Tables 12 and 13 as well as in Figures 10 and 11.

The highest total percentage canopy spread occurs in the 1 m stratum. While the 0.5 and 2 m strata are still fairly well developed, the 3 m stratum and above are poorly developed (Table 12). In the 1 m and 2 m strata *Colophospermum mopane*, *Combretum apiculatum* and *Dalbergia melanoxylon* (Table 13) have relatively high canopy cover percentages. Species of the 3 m, 4-5 m and >6 m height classes, among which *Colophospermum mopane* and *Combretum apiculatum* are important, have low canopy spread percentages.

The 0.5 m and 1 m height classes have the highest density. In the 0.5 m height class, sparse shrubs are most numerous whereas shrubs are most numerous in the 1 m height class (Table 12).

TABLE 12.
Percentage canopy spread in different strata and the mean number of individuals per hectare (indiv./ha) in different height classes of woody plant species in the *Colophospermum mopane*-*Themeda triandra* shrub savanna.

Stratum (m)	Percentage canopy spread								Mean number of indiv./ha					
	Total*	Growth form			Height class					Height class (m)	Total	Growth form		
		Tree	Sparse shrub	Shrub	>6m	4-5m	3m	2m	1m			0.5m	Tree	Sparse shrub
>6	0.23	0.19	0.04	—	0.23	—	—	—	—	>6	2	2	—	—
4-5	0.69	0.24	0.31	—	0.15	0.54	—	—	—	4-5	16	4	9	3
3	1.59	0.40	0.67	—	0.50	0.75	—	—	—	3	55	13	24	18
2	4.18	0.54	1.31	—	2.33	0.05	0.46	0.79	—	2	198	20	66	112
1	8.55	0.33	2.13	—	6.09	0.02	0.11	1.40	2.27	1	541	45	208	288
0.5	7.87	0.18	1.84	—	5.85	0.02	0.48	2.75	4.74	0-5	480	71	317	92
								2.02	4.29	Total	1 292	155	624	513

*Figures in this column are referred to in the text as "Total percentage canopy spread" values

TABLE 13.

Percentage canopy spread in different strata; mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species in the *Colophospermum mopane*-*Themeda triandra* shrub savanna.

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0,5
Colophospermum mopane	8,10	733	0,23	0,28	0,48	2,06	6,13	5,93
Combretum apiculatum	1,55	65		0,34	0,84	1,04	0,68	0,34
Dalbergia melanoxylon	0,83	140			0,03	0,38	0,59	0,51
Albizia harveyi	0,28	69			0,05	0,18	0,16	0,11
Cissus lonicerifolius	0,23	25				0,03	0,19	0,21
Commiphora africana	0,19	115					0,14	0,16
Combretum imberbe	0,16	9		0,05	0,10	0,12	0,07	0,04
Securinega virosa	0,11	23				0,03	0,08	0,09
Lonchocarpus capassa	0,11	11			0,02	0,04	0,05	0,08
Acacia nigrescens	0,09	12		0,02	0,03	0,05	0,06	0,05

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

Colophospermum mopane has the highest percentage apparent canopy cover, followed by *Combretum apiculatum* and *Dalbergia melanoxylon*, while *Colophospermum mopane*, *Dalbergia melanoxylon* and *Commiphora africana* have high densities (Table 13).

3. The *Colophospermum mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna

This community is found in the broken country in the Pafuri area, along the Madzaringwe and in the vicinity of the Machayi and Wambiya pans. It occurs on plains and on gentle to moderately steep (1-15°) north, east, southwest and south facing slopes between 230 and 475 m above sea level (Figs 1 & 9).

This community occurs on basalt, diabase, aeolian sand and gravel of the Quaternary. The loamy sand to clay soil is dark red brown to brown black and fine to medium textured. Up to 15% of the soil surface can be covered with stones. The soils are shallow to deep and the topsoil is apedal with a poorly developed blocky structure and a loose to friable consistency. The pH varies from 6.1 to 7.2. Although the soil usually contains a moderate soluble salt concentration it is strongly leached in parts. In most cases carbonates are present in the topsoil.

Floristic composition

Most of the tree species are from 4 to 5 m high, while some trees are up to 8 m high. The conspicuous trees are *Colophospermum mopane*, *Sclerocarya caffra* and *Combretum apiculatum*. The shrub layer which becomes up to 2 m high, includes *Colophospermum mopane*, *Combretum apiculatum*, *Grewia bicolor* and *Dichrostachys cinerea*. A few other common woody species are *Acacia nigrescens*, *Boscia albitrunca*, *Combretum mossambicense*, *Euclea divinorum*, *Markhamia acuminata*, *Securinega virosa*, *Commiphora mollis* and *Sterculia rogersii*.

The herbaceous component is characterised by *Digitaria eriantha* and *Schmidia pappophoroides* as well as *Panicum maximum*, *Aristida congesta* subsp. *congesta*, *Vigna unguiculata*, *Tephrosia polystachya*, *Phyllanthus pentandrus*, *Hibiscus micranthus* and *Solanum panduraeforme*. A few other associated species are *Heteropogon contortus*, *Aristida congesta* subsp. *barbicollis*, *Neuracanthus africanus*, *Fingerhuthia africana*, *Indigofera vicioides*, *Kyphocarpa angustifolia*, *Crotalaria virgulata* and *Euphorbia tetensis*.

Structure

The structural analysis of the woody component of this community is given in Tables 14 and 15 as well as in Figures 10 and 11.

The highest total percentage canopy spread is found in the 3 m stratum (Table 14). *Combretum apiculatum* has a high canopy spread percentage in this



FIG. 9.

The *Colophospermum mopane*–*Combretum apiculatum*–*Digitaria eriantha* open tree savanna.

stratum, whereas *Colophospermum mopane* has high percentages in the 3 m, 4–5 m and >6 m strata (Table 15). Up to the 2 m stratum sparse shrubs are most numerous and have the highest total percentage canopy spread; from the 3 m stratum trees predominate. Shrubs are relatively scarce and in the 4–5 m and >6 m height classes trees are most numerous (Table 14).

Colophospermum mopane, *Combretum apiculatum* and *Dalbergia melanoxylon* have high densities and *Colophospermum mopane* (13,47 %) and *Combretum apiculatum* (11,55 %) also have the highest percentage apparent canopy cover (Table 15),

COMPARISON OF STRUCTURE

In Figure 10 the first three communities (1.1; 1.2 and 1.3) have the same basic pattern for the total percentage canopy spread: there is an increase from the 0,5 m stratum up to the 2 m stratum whereafter the values decrease progressively with increasing stratum height.

In community 3 the highest total percentage canopy spread occurs in the 3 m stratum. The Shilahladonga variation (a) of community 2.1 has more or less the same percentage canopy spread as community 2.2. However, in community 2.1

TABLE 15.

Percentage canopy spread in different strata, mean number of individuals per hectare (indiv./ha) and the percentage apparent canopy cover (p.a.c.) of a few species* in the *Colophospermum mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna.

Plant species*	p.a.c.	indiv./ha	Percentage canopy spread					
			Stratum (m)					
			>6	4-5	3	2	1	0.5
Colophospermum mopane	13.47	928	4.45	6.30	5.33	4.02	3.74	2.44
Combretum apiculatum	11.55	453	0.10	3.03	8.19	8.22	3.22	1.08
Grewia bicolor	0.86	54				0.64	0.68	0.55
Sclerocarya caffra	0.82	11	0.59	0.79	0.62			0.01
Acacia nigrescens	0.71	109	0.31	0.19	0.15	0.18	0.17	0.25
Dalbergia melanoxylon	0.47	163			0.16	0.28	0.26	0.26
Combretum mossambicense	0.30	121				0.02	0.07	0.27
Dichrostachys cinerea	0.23	52				0.11	0.13	0.09
Boscia albitrunca	0.22	21		0.13	0.16	0.02	0.05	0.03
Cissus lonicerifolius	0.20	18				0.02	0.20	0.11

*Only the ten species with the highest percentage apparent canopy cover (p.a.c.)

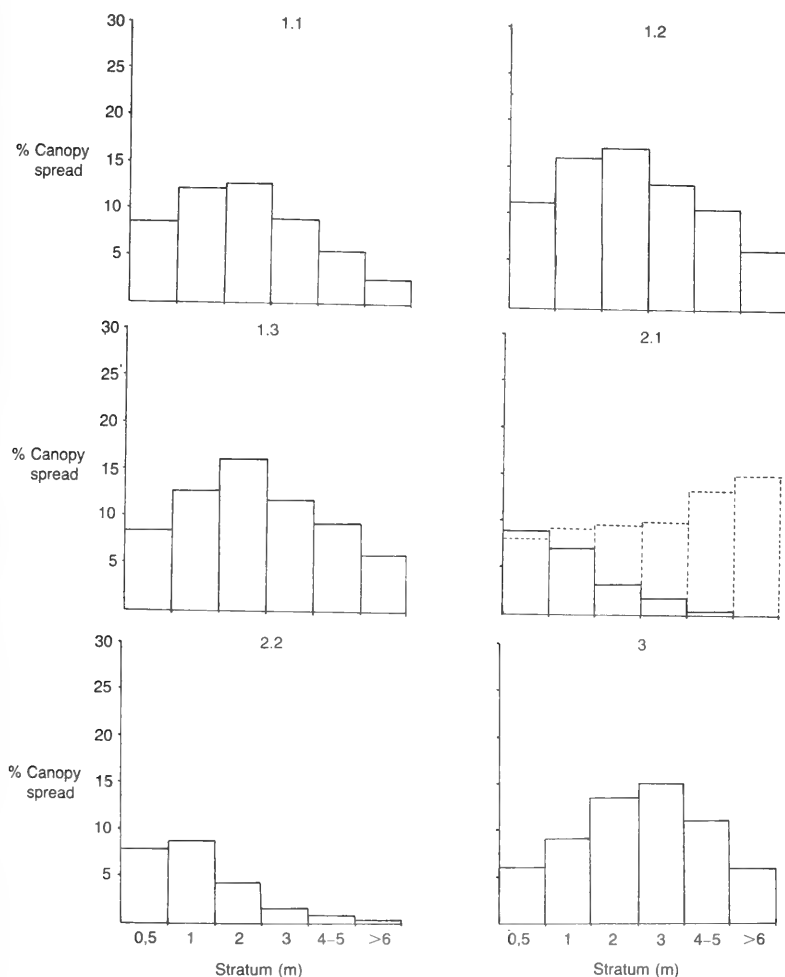


FIG. 10.

A diagrammatic presentation of the total percentage canopy spread of woody plants in different strata of the *Colophospermum mopane* communities.

- 1.1 The *C. mopane*-*Acacia tortilis*-*Urochloa mosambicensis* tree savanna
- 1.2 The *C. mopane*-*Euclea divinorum*-*Enteropogon macrostachyus* tall tree savanna
- 1.3 The *C. mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna
- 2.1 The *C. mopane*-*Enneapogon scoparius* shrub savanna
 - a. Shilahlandonga variation
 - b. Matule variation
- 2.2 The *C. mopane*-*Themeda triandra* shrub savanna
3. The *C. mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna

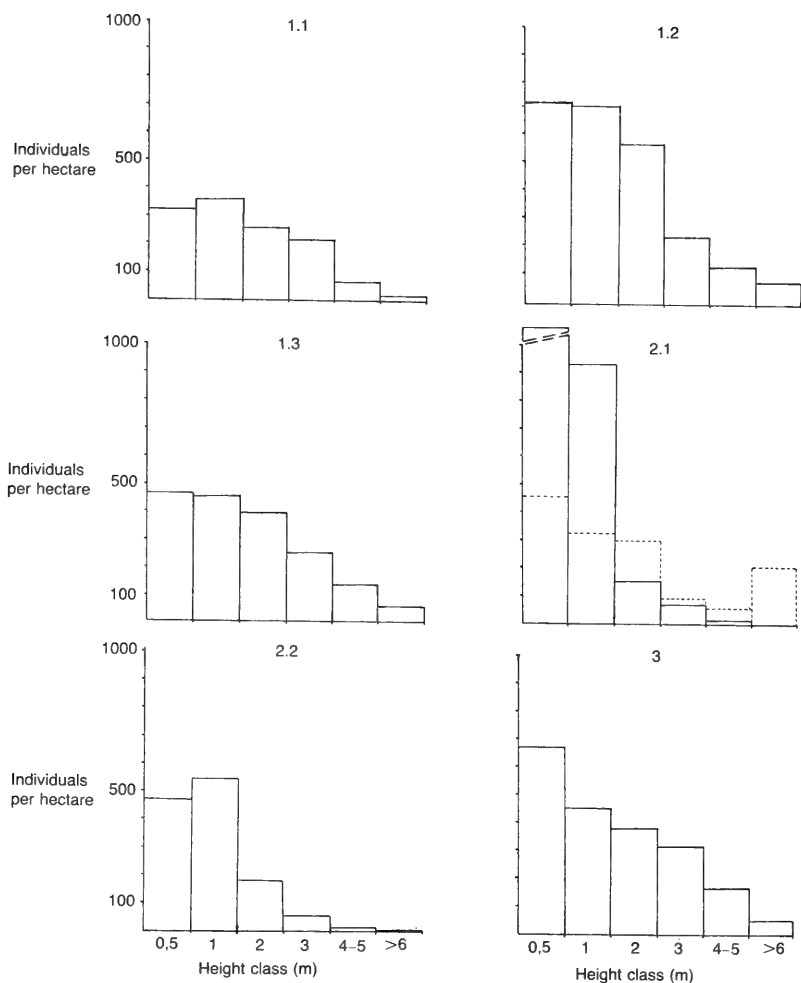


FIG. 11.

A diagrammatic presentation of the mean total individuals per hectare in different height classes of the woody plants of the *Colophospermum mopane* communities.

- 1.1 The *C. mopane*-*Acacia tortilis*-*Urochloa mosambicensis* tree savanna
- 1.2 The *C. mopane*-*Euclea divinorum*-*Enteropogon macrostachyus* tall tree savanna
- 1.3 The *C. mopane*-*Commiphora glandulosa*-*Seddera capensis* open tree savanna
- 2.1 The *C. mopane*-*Enneapogon scoparius* shrub savanna
 - a. Shilahladonga variation
 - b. Matule variation
- 2.2 The *C. mopane*-*Themeda triandra* shrub savanna
3. The *C. mopane*-*Combretum apiculatum*-*Digitaria eriantha* open tree savanna

(a) more individuals per hectare are found in the 0.5 m and 1 m height classes than in community 2.2. Compared to the other *Colophospermum mopane* communities these two communities have relatively low canopy spread percentages in the 4–5 and >6 strata. The Matule variation (b) of community 2.1 has a higher total percentage canopy spread in the 4–5 m and >6 m strata than the Shilahlandonga variation (a).

In general the highest number of individuals per hectare is found in the 0.5 m and 1 m height classes (Fig. 11) with a reduction in numbers in the higher height classes. There is however, a marked variation in numbers of individuals per hectare between the different communities.

The results reveal a large amount of structural variation between communities as well as within communities. Some communities differ floristically but they have the same structure, whereas others are floristically similar yet differ structurally e.g. *Colophospermum mopane*–*Enneapogon scoparius* community (Fig. 10).

CONCLUSION

In savanna plant communities, as in all living societies, there is perpetual competition for survival between individuals and evolution towards a more highly organised type of association in which the abiotic, floristic and structural components are in equilibrium with one another.

Successful management of large areas covered with natural vegetation depends largely on a knowledge of the composition of the vegetation, the extent to which it is being utilised and the changes which take place in response to differential use by herbivores and fire (Walker, 1976). Where fire and utilisation have the greatest influence on savanna vegetation (Glover, 1968) it is necessary to study the floristic composition and structure in areas that are subjected to different intensities of burning and grazing in order to observe the changes brought about by such treatments.

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FIELD STUDIES ON DIURNAL LEAF DIFFUSIVE RESISTANCE OF MANGROVE LEAVES AT VARIOUS SOIL MOISTURE TENSIONS AND PHOTOSYNTHETICALLY ACTIVE RADIATION

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ABSTRACT

Diurnal trends in leaf diffusive resistance of two mangrove species, *Avicennia marina* (Forsk.) Vierh. and *Bruguiera gymnorhiza* (L.) Lam., were investigated at varying moisture levels and photosynthetically active radiation (PAR). Generally, diffusive resistance decreased from early morning till midday as PAR increased. After midday, resistance increased primarily as a result of decreasing PAR and increasing soil moisture tensions. Tidal inundation of the mangroves did not have any measureable effect on diffusive resistance at low PAR and at low soil moisture tensions. Under conditions of high PAR and high soil moisture tensions tidal coverage of the swamp relieved soil moisture stress and resulted in decreased leaf diffusive resistance.

UITTREKSEL

VELDSTUDIES VAN DAAGLIKSE BLAARDIFFUSIEWEERSTAND VAN MANGLIETBLARE BY VERSKILLEND VOGSPANNINGS EN FOTOSINTETIESE-AKTIWE STRALING

Daaglikse verloop van blaardiffusieweerstand van twee manglietsoorte, *Avicennia marina* (Forsk.) Vierh. en *Bruguiera gymnorhiza* (L.) Lam. is by wisselende voggehaltes en fotosinteties-aktiewe straling (FAS) ondersoek. Oor die algemeen het diffusieweerstand afgeneem vanaf vroeg oggend tot middag, soos FAS toegeneem het. Na die middag-uur het weerstand toegeneem, primêr as gevolg van vermindering in FAS en toenemende grondvogspannings. Getyoorstrominge van die mangliete het geen meetbare uitwerking op diffusieweerstand by lae FAS en lae grondvogspannings gehad nie. Onder omstandighede van hoë FAS en hoë vogspannings het getybedekking van die moeras die grondvognoed verlig en verminderde blaardiffusieweerstand tot gevolg gehad.

INTRODUCTION

Mangroves in intertidal zones are regularly inundated by sea water which has a high osmotic potential. Yet, very little information is available on the stomatal responses of these plants to marked diurnal fluctuation in substrate moisture levels and osmotic potentials. Apparent transpirational rhythms in the white mangrove, *Avicennia marina* were investigated using simple potometric methods (Lewis & Naidoo, 1970; Steinke, 1979). The disadvantage of the potometric method is that it does not provide an absolute figure for the loss of water by the plant. In addition, a potometer records water absorption by a transpiring

branch. Conclusions drawn from water absorption data from the base of a transpiring branch cannot be directly applied to stomatal responses unless data are recorded at the leaf surface.

Studies on water relations in mangroves have been concerned mainly with the effects of salinity. Scholander *et al.* (1965) and Scholander (1968) determined osmotic potentials and xylem potentials in some mangrove species. Miller (1974) reported that stomata of mangrove species in Florida respond differently to different salinities.

The aim of this investigation was to determine the diurnal adjustments in stomatal responses of two local mangrove species, *Avicennia marina* and *Bruguiera gymnorhiza*, to varying soil moisture levels and photosynthetically active radiation.

MATERIAL AND METHODS

Field measurements were carried out during April and May of 1979 at the Beachwood mangrove area, Durban. Mangrove trees 3.5 to 4.5 m tall were selected for data collection. To investigate the effects of varying soil moisture tensions on stomatal responses, measurements were made on trees growing in soils that were continuously moist and regularly inundated, and on trees that were growing in relatively dry areas inundated only during high spring tides. The leaves selected for measurements were located at the tips of branches that were approximately 1.5 m above ground level. All measurements were made hourly.

Leaf diffusive resistances were measured with a diffusion porometer (Lambda Instruments Inc., Model No. Li 65, Lincoln, Nebraska) with a horizontal sensor cup. The porometer was calibrated by prescribed procedures both before and after measurements were taken. To ensure that porometer data were reliable, procedures and precautions described by Kanemasu *et al.* (1969) and Morrow & Slatyer (1971) were followed. Since both *Avicennia* and *Bruguiera* are hypostomatous, diffusive resistance was determined for the abaxial surface only. Adaxial resistance for both mangrove species was usually greater than 50 s cm^{-1} . The stomatal frequency for both species was about 180 stomata mm^{-2} .

During each porometer reading measurements were made of the light incident on the adaxial surface of the leaf with a quantum light meter (Lambda Instruments Inc., Model No. Li 185, Lincoln, Nebraska). The quantum sensor measures photosynthetically active radiation (PAR) in units of microEinsteins per square metre per second ($\mu\text{E m}^{-2} \text{ s}^{-1}$).

Soil moisture tension was determined by Gallenkamp soil tensiometers which were buried in the ground to a depth of 200 mm at the base of trees which were being sampled. The tensiometers were prepared by following procedures recommended by the manufacturers. Usually, tensiometers were left overnight for equilibration.

Stomatal imprints were obtained with cellulose acetate diluted with amyl acetate. The imprints were removed with transparent sticky tape, placed on stubs, coated with gold and examined with a scanning electron microscope.

All measurements were made on clear sunny days. Wind speed, relative humidity, temperature, tidal levels and salinity of the tidal water were also noted. Temperatures during data collection varied between 25° to 30°C.

RESULTS AND DISCUSSION

In most cases results were similar for *Avicennia* and *Bruguiera*; therefore the results presented for one are representative of the other.

Data in Figure 1 represent typical responses of *Avicennia* on a day on which

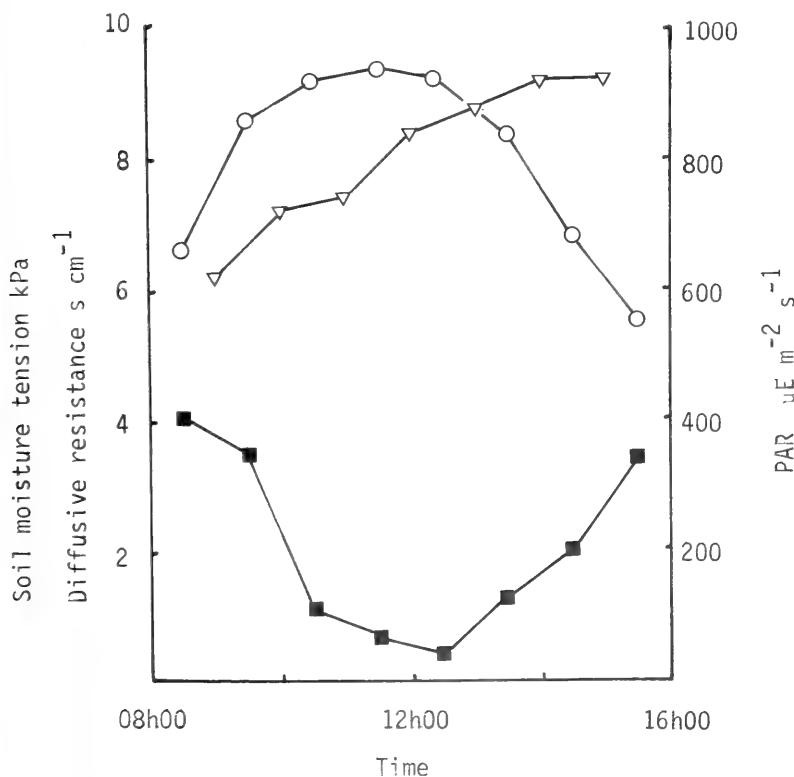


FIG. 1.

Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 10/4/79. No tidal coverage.

no tidal inundation occurred. Leaf diffusive resistance decreased from 08h00 to 12h00 in response to increasing PAR. During the sampling period the soil moisture content was below field capacity (>6 kPa). Thereafter, leaf diffusive resistance increased as a result of decreasing PAR and increasing soil moisture tension. Plants had probably reached a state of incipient wilting at high soil moisture tensions resulting in stomatal closure.

Similar results were obtained for *Bruguiera*. Hourly observations of stomatal imprints (Fig. 2 A & B) for *Bruguiera* confirmed that stomata were maximally open at midday. At maximal stomatal opening the width of the aperture was $11\mu\text{m}$.

Unfortunately, it was not possible to make stomatal imprints of the abaxial surface of *Avicennia* leaves because of the numerous pedicellate hairs present on the surface (Fig. 2 C & D). Others (Lewis & Naidoo, 1970; Steinke, 1979) reported that *Avicennia* exhibits a mid-morning maximum. However, these workers used potometric techniques which measured apparent transpiration and not direct loss of water from the leaf surface. Diffusion porometers on the other hand characterize responses of stomata with direct reference to the transpiration process (Van Bavel *et al.*, 1965).

Trends in diffusive resistance for *Avicennia* under very low soil moisture tensions and low PAR are shown in Figure 3. Diffusive resistance decreased with increase in PAR, as in Figure 1, reaching minimum resistance at noon. Subsequent rapid decrease in PAR caused a rapid increase in diffusive resistance. Tidal coverage of the swamp during the early afternoon had no effect on diffusive resistance probably because of the low soil moisture tension. That the soils were waterlogged during the whole morning is indicated by soil moisture tension values of less than 4 kPa. Similar results were obtained for several *Avicennia* and *Bruguiera* trees under similar conditions of PAR and soil moisture tension.

In Figures 4 and 5 stomatal responses followed the usual pattern, the resistance decreasing till midday as PAR increased. After midday the leaf resistance began to increase primarily as a result of decreasing PAR and increasing soil moisture tension. Tidal inundation of the swamp resulted in a second decrease in diffusive resistance for both *Bruguiera* (Fig. 4) and *Avicennia* (Fig. 5).

In *Bruguiera* the tidal effect on diffusive resistance occurred between 14h00 and 14h30. At this time the soil moisture tension was 10,6 kPa, which is well below field capacity, and the PAR value was $530\mu\text{Em}^{-2}\text{s}^{-1}$.

In *Avicennia* the tidal effect occurred after 13h00. At 13h00 the soil moisture tension was 8,7 kPa, which is again well below field capacity, and PAR was $780\mu\text{Em}^{-2}\text{s}^{-1}$. Decrease in diffusive resistance during tidal inundation thus occurred at high soil moisture tension and high PAR. The tidal effect on diffusive resistance was only observed on trees growing in relatively dry areas and well exposed to PAR. An incoming tide had no effect on diffusive resistance in Figure 3 because the soils were waterlogged and PAR was low ($375\mu\text{Em}^{-2}\text{s}^{-1}$).

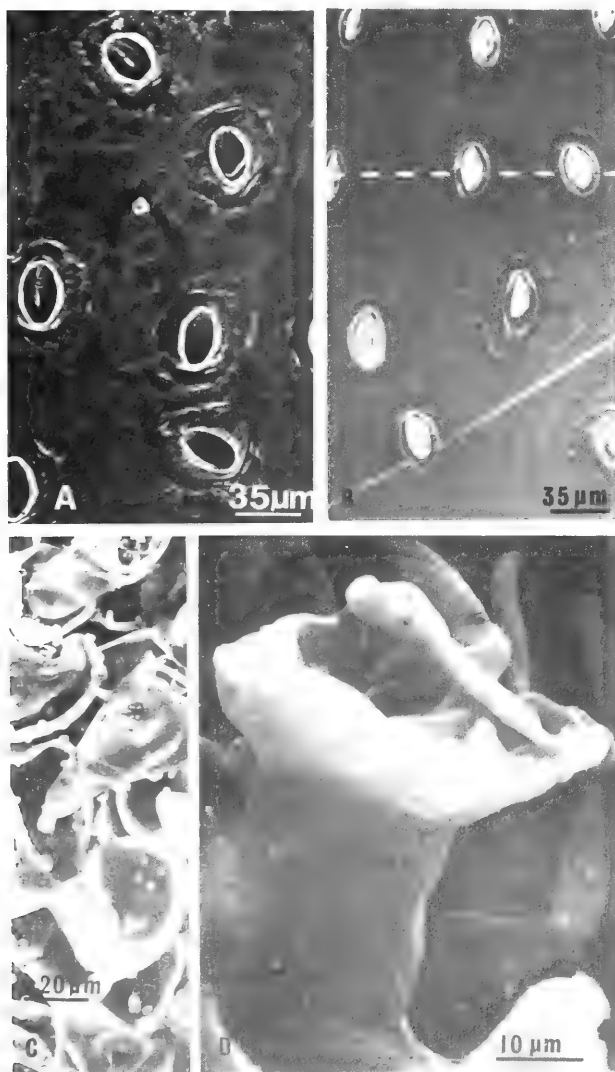


FIG. 2
Scanning electron micrographs of abaxial leaf surfaces.

- A. stomata of *B. gymnorrhiza* at 09h00
- B. stomata of *B. gymnorrhiza* at 12h00
- C. pedicellate hairs on leaf of *A. marina*
- D. a single pedicellate hair of *A. marina*

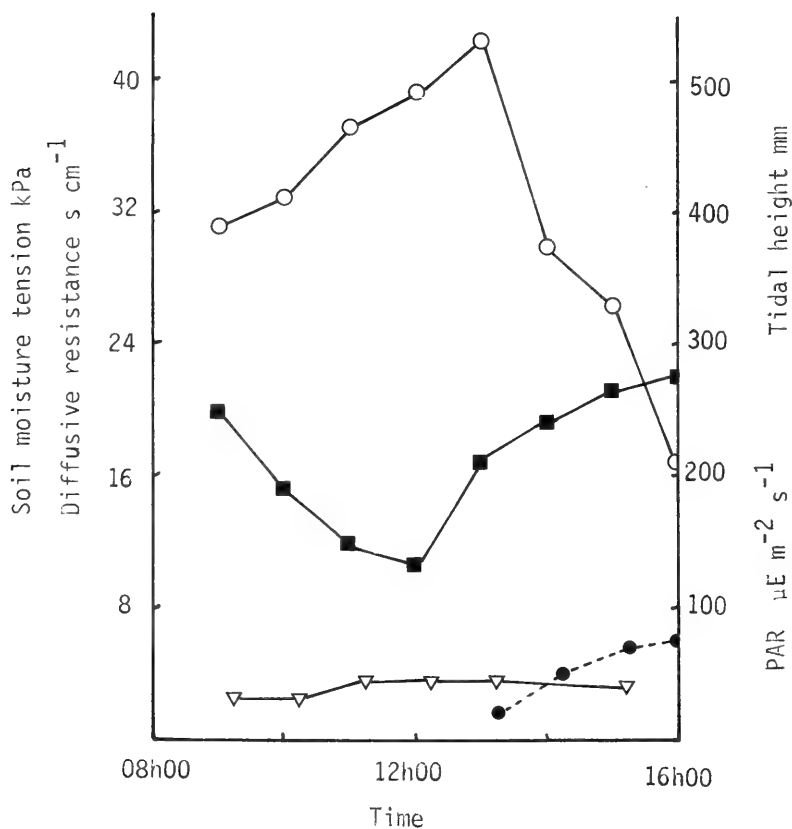


FIG. 3.
Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 22/5/79. Tidal coverage (●—●—●).

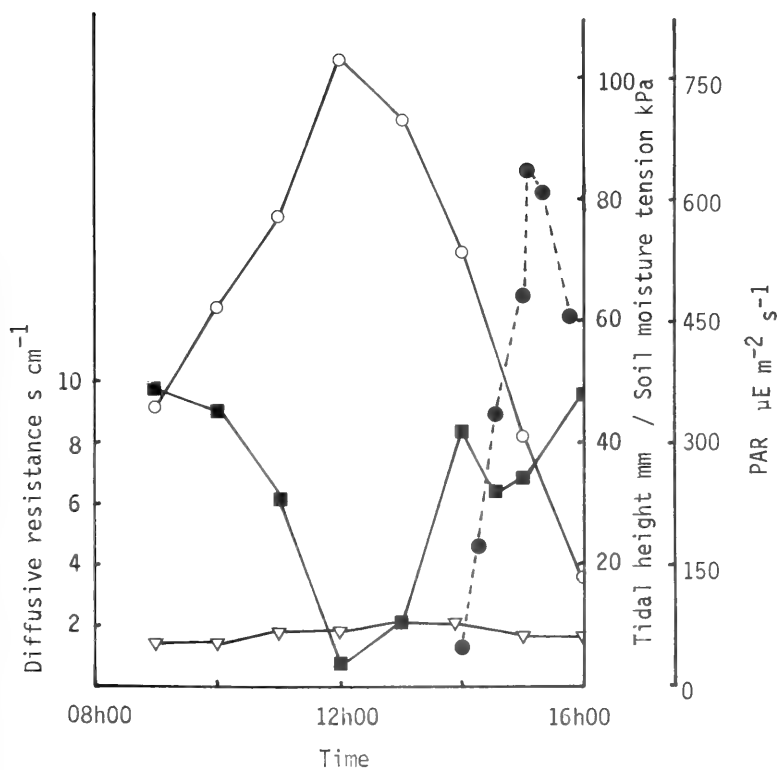


FIG. 4.

Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *B. gymnorrhiza* on 10/4/79. Tidal coverage (●—●).

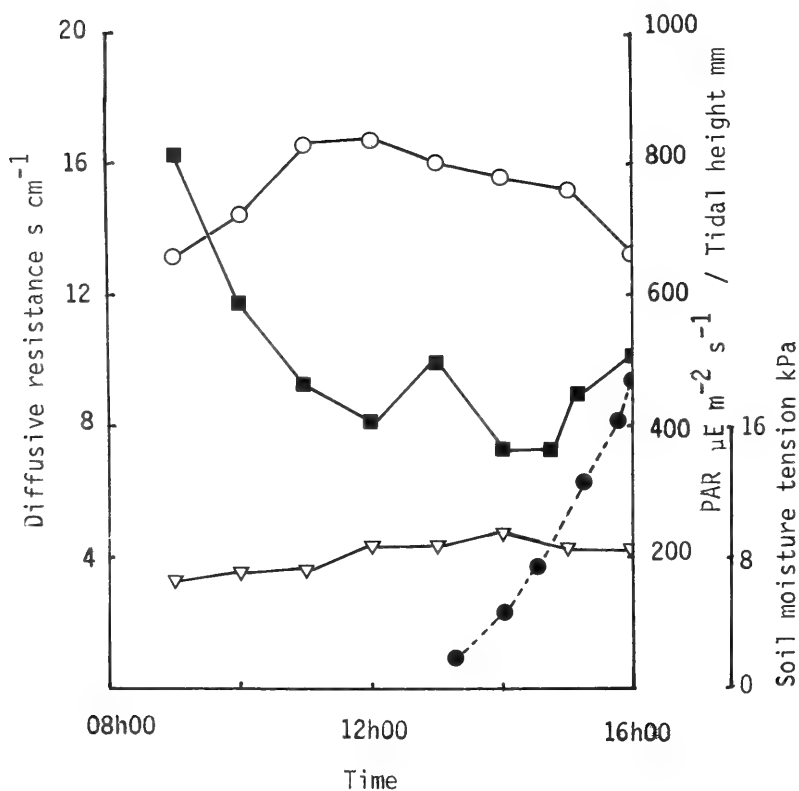


FIG. 5.

Diurnal trends in diffusive resistance (■—■), PAR (○—○) and soil moisture tension (▽—▽) of *A. marina* on 11/5/79. Tidal coverage (●-----●).

An increase in apparent transpiration rate in *A. marina* during tidal inundation was reported previously (Lewis & Naidoo, 1970).

The significant relationship between diffusive resistance and PAR for *Bru-guiera* under shaded and non-shaded conditions is shown in Figure 6. The regression line for shaded conditions shows that the resistance is greater at low PAR. For trees well exposed to PAR the diffusive resistance is considerably reduced. Thus there is a trend towards lower resistance at high PAR.

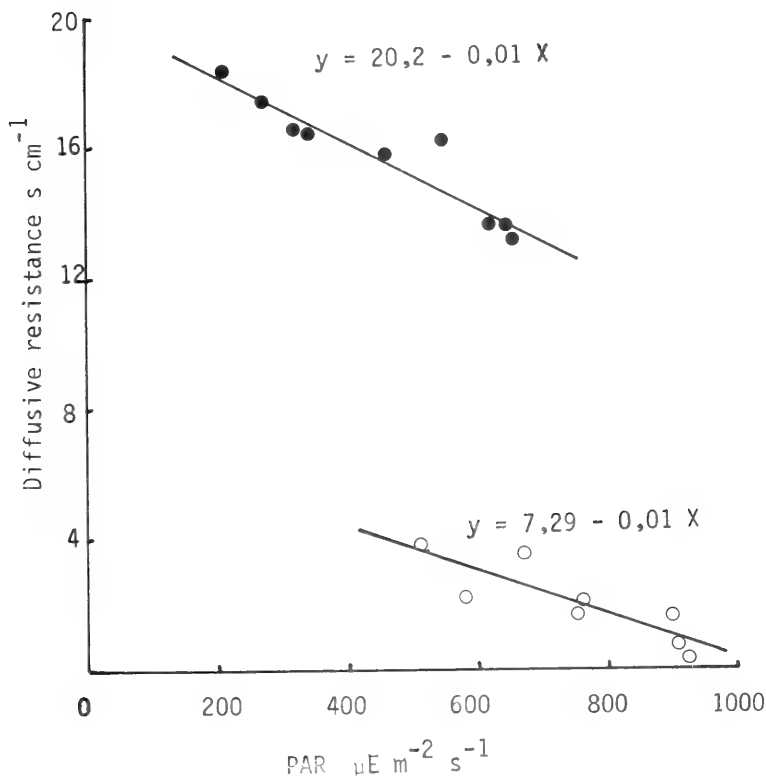


FIG. 6.

The relationship between leaf diffusive resistance and PAR for *B. gymnorrhiza* under shaded (●) and non shaded (○) conditions. Each point is an average of three leaves.

Although mangroves inhabit a continuously moist environment their stomatal responses are similar to those of many other plants. In the field, stomatal responses are largely governed by irradiance and soil moisture stress (Meidner & Mansfield, 1968; Kanemasu & Tanner, 1969; Teare & Kanemasu, 1972; Denmead & Miller, 1976). These two factors largely determine the water potential gradient along the soil-plant-atmosphere continuum. Most plants would be under stress if swamped by sea water which has an osmotic potential of -2400 kPa. However, mangrove xylem sap has been shown to possess negative pressures of up to 6080 kPa (Scholander *et al.*, 1965). This supports our observation that tidal coverage of mangroves actually relieves soil moisture stress and subsequently results in decreased leaf diffusive resistance.

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THE SUBTERRANEAN INTERMEDIARY ORGANS OF *DIOSCOREA COTINIFOLIA* KUNTH: 2. ANATOMY OF THESE ORGANS IN COMPARISON WITH THAT OF A TYPICAL ROOT AND SHOOT

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ABSTRACT

A comparison is made between the intermediary organs, (i.e. the tuber and cylindrical organs) and the roots and shoots. The most remarkable features of the root and the shoot are specially mentioned. Anatomically the intermediary organs have a rootlike feature but are in some respects similar to the shoot. This anatomical investigation, however, supplies enough evidence of the uniqueness of the specialised tuber system of *D. cotinifolia*, confirming the idea of it being intermediate between a typical root and a typical shoot. Detailed descriptions of the vascular elements are supplied.

UITTREKSEL

DIE ONDERGRONDSE INTERMEDIËRE ORGANE VAN *DIOSCOREA COTINIFOLIA* KUNTH: 2. ANATOMIE VAN HIERDIE ORGANE IN VERGELYKING MET DIE VAN 'N TIPIESE WORTEL EN STINGEL

'n Vergelyking tussen die intermediêre organe (d.i. die knol en silindriese organe) en die wortels en stingels word getref. Die opvallendste kenmerke van die wortel en die stingel word spesiaal vermeld. Anatomies het die intermediêre organe 'n wortelagtige kenmerk maar kom in sommige opsigte ooreen met die stingel. Hierdie anatomiese ondersoek het egter genoeg getuigenis van die uniekheid van die gespesialiseerde knolsisttem van *D. cotinifolia* gelever om die idee dat dit intermediêr tussen 'n tipiese wortel en 'n tipiese stingel is, te onderskraag. Gedetailleerde beskrywings van die vaatelemente word voorsien.

I. INTRODUCTION

In 1977 Von Teichman und Logischen, Robbertse and Van der Schijff described the origin of the subterranean intermediary organs of *Dioscorea cotinifolia* Kunth. Simultaneously and independently Cartoni-Cretton (1977) made similar observations on the tuber of *Tamus communis* L., a close relative of the genus *Dioscorea*, and also found that the tuber originates from the hypocotyl.

The underground structures which were described for *D. cotinifolia* by Von Teichman *et al.*, (1977) were: (1) roots; (2) the *tuberous* intermediary organs; and (3) the usually long, *cylindrical* intermediary organs closely resembling roots. For the sake of brevity we will refer to them as roots, *tubers* and *cylindrical organs* respectively. The latter two which include the crown of the tuber, comprise the specialised tuber system which bears the adventitious roots. In this anatomical comparison of the intermediary organs with typical roots and the

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typical internodes of the aerial shoot (referred to as shoots) we provide further evidence of their unique nature.

Neither Archibald (1967) nor Ayensu (1972) described the anatomy of the underground organs of *D. cotinifolia* and since Ayensu mentioned that these organs were generally neglected, it is considered appropriate to describe their anatomy in detail here. Figures of the tracheary elements are not supplied because the figures published by Shah *et al.*, (1967) and Tan and Rao (1974) are considered to be adequate. For convenience a short introductory description of the root and the shoot is also provided.

II. MATERIAL AND METHODS

The material used, (see Von Teichman and Logischen *et al.*, 1977) was dissected and fixed in 6 % glutaraldehyde at 0°C. The preparation was done according to Feder and O'Brien (1968). The monomer mixture however consisted of 96 % (v/v) hydroxyethyl methacrylate (that is, the 96 % HEMA was purified to remove most of the methacrylic acid); 5 % (v/v) polyethylene glycol 200 and 0.1 % (w/v) azobis-iso-butyronitrile. The 2 µm sections were cut with glass knives on a MT-1 Porter Blum ultramicrotome. Sections were stained with periodic acid—Schiff's stain (PAS) followed by toluidine blue (Feder and O'Brien, 1968). Staining for lipids was done with a saturated solution of sudan black B in 70 % ethanol, rinsing briefly with 70 % ethanol and mounting the wet sections in glycerine jelly.

Large tuber pieces and other similar material, were dehydrated in a tertiary butyl alcohol series. Paraplast (melting point = 56–57°C, obtained in pellet form) was used for infiltration and embedding.

The dewaxed sections were also stained with toluidine blue. Small pieces of the organs were macerated by briefly heating in a mixture of 50 cm³ concentrated nitric acid and 1 g potassium chlorate. After rinsing in water and subsequently in 50 % ethanol the material was stained with 1 % safranin O in 50 % ethanol. An ethanol rinse preceded mounting in glycerine.

The section used in Figure 2B was FAA-material cut free-hand, air-dried, mounted, sputter-coated with gold and photographed with a Philips SEM 500 at 12kV.

III. OBSERVATIONS AND DISCUSSION

1. The root

The uniseriate rhizodermis with root hairs, encloses an exodermis, a parenchymatous central cortex and an endodermis (Fig. 1A). The cortex cells outside the endodermis usually have thickened inner tangential walls (Fig. 1B). The pericycle is lignified especially adjacent to the phloem groups. The stele is polyarch with huge metaxylem elements lying scattered in the pith (Fig. 1A).

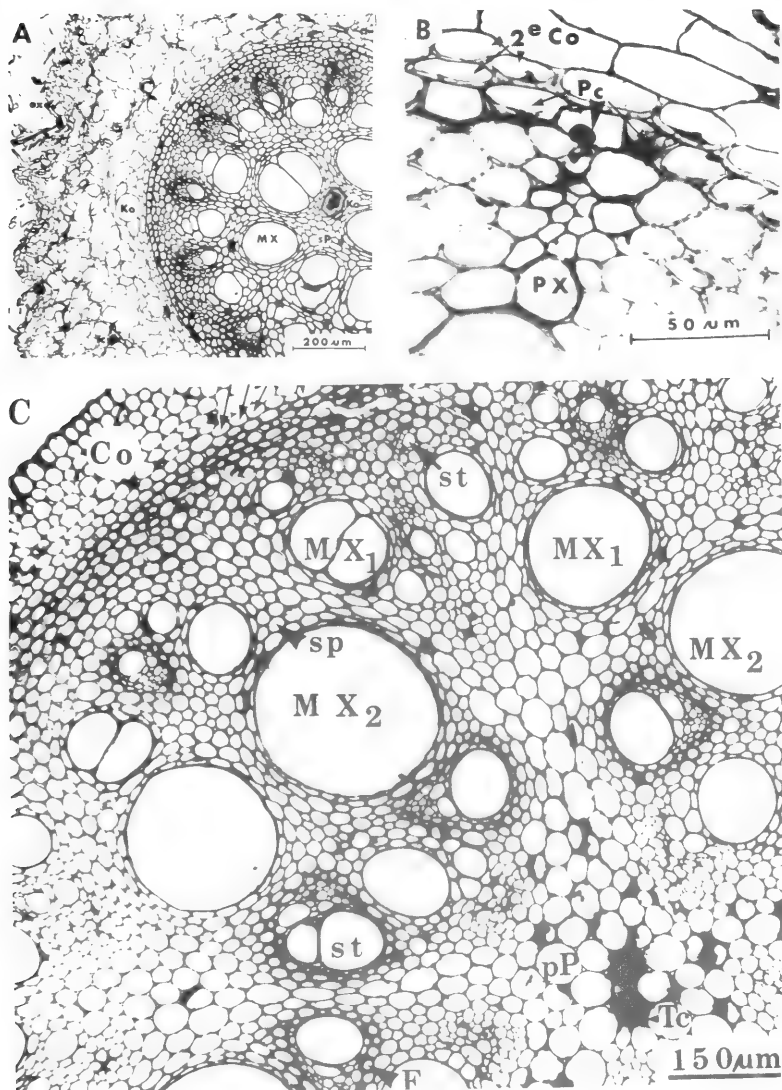


FIG. 1.

Transverse sections of the root and the shoot. A: Part of a mature root, exo—exodermis; Ko—idioblast; MX—metaxylem vessel; sP—sclerenchymatous parenchyma; B: A small part of a mature root, 2e Co—cortex layer outside endodermis; Pc—passage cells; PX—protoxylem vessel; C: Part of a mature shoot, small arrows—endodermoid layer; Co—cortex; F—fibre; MX₁ large metaxylem vessel in common vascular bundle; MX₂ the same in the cauline vascular bundle; pP—parenchymatous pith; sp—sclerenchymatous parenchyma; st—sieve tube; Tc—tanniferous cell.

2. The shoot

Inside the single-layered epidermis lies the cortex, the innermost layer representing the endodermoid layer. Inside this endodermoid layer is a mechanical tissue, of 6–8 layers of mainly lignified parenchyma, which encircles the vascular bundles. Several or single small common vascular bundles alternate with large cauline vascular bundles (Fig. 1C).

3. A comparison of the intermediary organs with the root and shoot

3.1 The epidermis or outermost cell layer

Unicellular structures resembling root hairs occur in the uniseriate epidermis of the young cylindrical organs (Fig. 2C).

Stomata and a cuticle are absent in this epidermis.

The epidermal cells of the root are dome-shaped with slightly thickened outer tangential walls. In mature cylindrical organs and tubers the epidermis has already been shed by the peripheral periderm.

The single-layered epidermis of the shoot consists of more or less spherical cells with rather thick, often lignified and pitted walls. Stomata are present and the thick (1.9 μm), often ridged cuticle stretches right into the substomatal chamber (Fig. 2A). The guard cells show distinct outer and inner ledges (Fig. 2A, inset). The subsidiary cells are usually distinctly radially elongated.

3.2 The outer ground tissue and cortex

Histochemical tests revealed no *suberin* or *lignin* in the hypodermal cells of young cylindrical organs. The outer ground tissue in these organs consists of thin-walled parenchyma. The phellogen, a continuous cambium, originates in about the seventh layer of ground tissue and initially forms two to three layers of phellem cells (Fig. 2C). Very little or no phelloderm is formed by the phellogen. In the tuber of *D. cotinifolia* the phellogen arises in the outermost ground tissue. This confirms the results of Martin and Ortiz (1963) on *D. floribunda* and *D. spiculiflora*. Other workers, like Bucherer (1889), state that the initials of the phellogen arise in the epidermis.

In the cylindrical organs of *D. cotinifolia*, the cell walls of the ground tissue between the epidermis and phellem become lignified. In other *Dioscorea* species this outer tissue is suberized (Sharma, 1974). The outermost tissue of old cylindrical organs and tubers of *D. cotinifolia* is a phellem of 6 to 12 layers.

In the cylindrical organs, a second lateral meristem is usually situated at about the tenth cell layer of parenchymatous ground tissue inside the phellogen (Figs 2C and 3). It is by no means a continuous cambium but merely a discontinuous meristematic zone. As a result of successive cell divisions within this zone, groups of small cells are formed which later differentiate into secondary vascular bundles (Figs 2C and 3). Secondary ground tissue is also formed by this meristem.

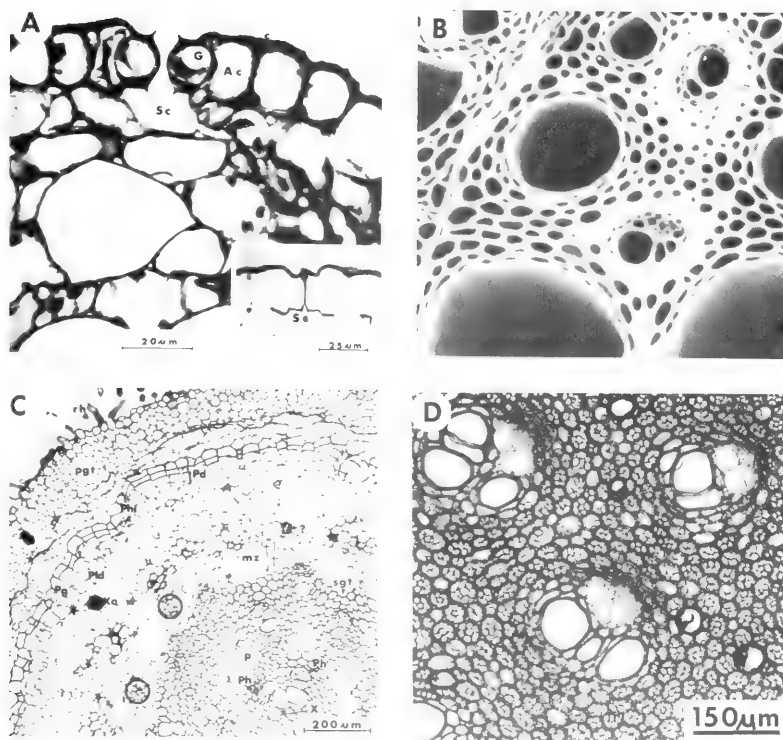


FIG. 2.

Transverse sections of the shoot and the cylindrical intermediary organ. A: Stomata of a shoot, Ac—subsidiary cell; G—guard cell; Sc—substomatal chamber, the inset is a GMA-section stained with Sudan Black B; B: Part of a cauline vascular bundle in the shoot showing the fibres surrounding the phloem unit (S.E.M. micrograph); C: A young cylindrical organ; Ko—idioblast with mucilage; mz—lateral meristem or meristematic zone; p—parenchymatous ground tissue; Pd—periderm; Pg—phellogen; Ph—phloem; Pld—phelloderm; rh—piliferous layer; sgt—sclerenchymatous ground tissue; X—xylem vessels or tracheids; circles—small groups of cells; D: Part of the sclerenchymatous inner ground tissue, filled with starch, and 3 vascular bundles in an older cylindrical organ.

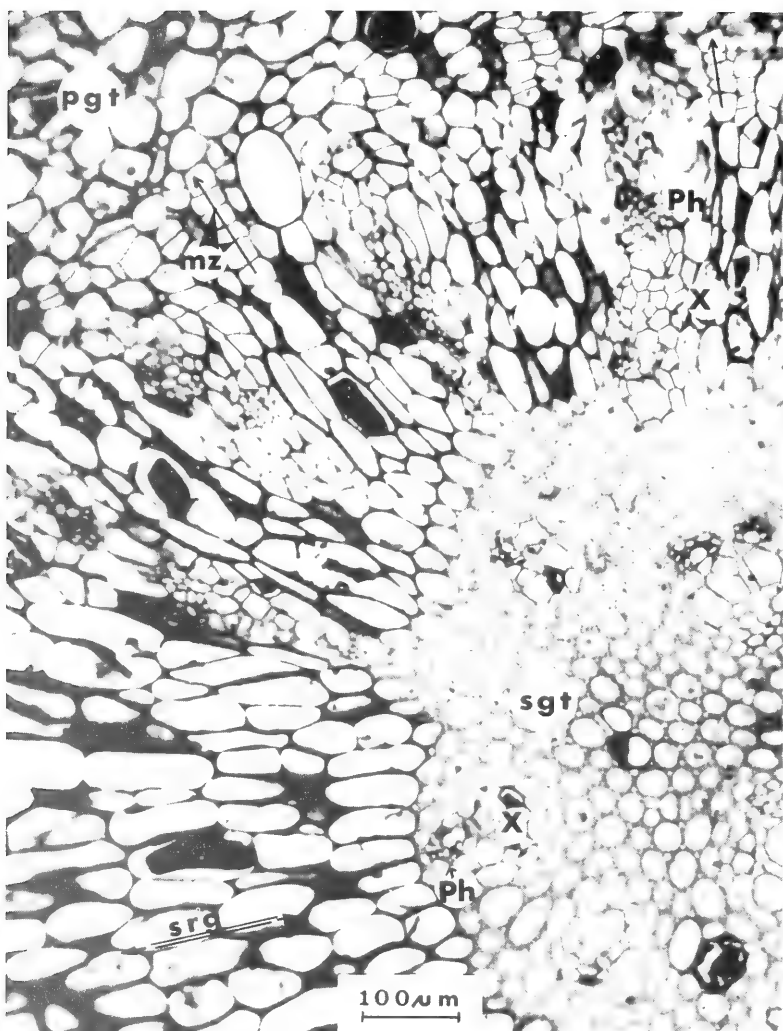


FIG. 3.

Transverse section of an older cylindrical organ, mz—lateral meristem; pgt—parenchymatous outer ground tissue; Ph—phloem unit; sgt—sclerenchymatous inner ground tissue; srg—cells radially elongated; x—xylem.

Tomlinson and Zimmermann (1967) described the origin of these secondary vascular bundles in the secondary ground tissue of monocotyledons as follows: "a vertical series of cambial derivatives divides longitudinally in various planes. From this prodesmogen strand tracheids, sieve-tubes and parenchyma differentiate". In the case of *D. cotinifolia* we have not confirmed their statement that the secondary vascular bundles usually do not include vessels.

Observations on very young tubers of *D. sylvatica* (Von Teichman und Logischen, 1973) confirmed the results of Bucherer (1889) and Martin and Ortiz (1963) regarding the origin of this lateral meristem. Martin and Ortiz stated, that the cambium as they called it, "is an extension and specialization of the primary thickening meristem". The latter begins very close to the promeristem in the tuber crown. This probably also applies to *D. cotinifolia* tubers. In the older tubers, however no distinct lateral meristem or meristematic zone can be distinguished.

Sharma (1974) also found that the "primary thickening meristem" is rather indistinct in mature tubers. In the apex of a young cylindrical organ of *D. cotinifolia* which had just started to tuberize, a distinct endogenous primordium (Fig. 4A) was noted within the meristematic zone. Such a primordium may develop into adventitious shoots, adventitious roots or secondary cylindrical organs (Von Teichman und Logischen *et al.*, 1977).

A section through the apex of this cylindrical intermediary organ shows that it is neither like a root nor like a shoot apex (Fig. 4A). No calyptra is present and the procambial strands are scattered. No leaf primordia are present and the lateral primordium (dark spot in Fig. 4A) is of endogenous origin. It is very close to the tip of the apex and its origin is slightly similar to that of root buds described by Peterson (1975). Our section is very similar to that of the tuber apex of *D. floribunda* (Sharma, 1980).

We therefore agree with Koch and Bruhn (1962) who stated that the tuber apex is not homologous with a root or a shoot apex, and that growth results from exceptionally actively dividing cells within the lateral meristem.

Martin and Ortiz (1963) observed that "the dorsal cortex of isolated tuber pieces is able to develop new shoot primordia, making possible the propagation of these species by tuber cuttings".

In some of the older tubers of *D. cotinifolia* a discontinuous band of sclereids is present in the inner part of the outer ground tissue. This ground tissue consists of thin-walled parenchyma with well-developed intercellular spaces. Tanniferous cells and idioblasts, containing crystals in the form of raphide bundles surrounded by mucilage (henceforth referred to as idioblasts) occur throughout the ground tissue of all the intermediary organs.

The exodermal cells in the root are two to three times the size of the epidermal cells and a distinct continuous suberin lamella is present in their walls. Very large idioblasts occur in the otherwise thin-walled cortex while one or

sometimes two cell-layers outside the endodermis usually have thickened inner tangential cell walls. In mature roots these cell walls become lignified (Fig. 1B).

In 1889, Bucherer already reported the presence of a characteristic layer or sheath ("Aussenscheide") in Dioscoreaceae roots just outside the endodermis, which he called "Schuttscheide". He also quite correctly mentioned that the degree of thickening of the cell walls of these cortex cells was related to the age of the root. The innermost cortical layers of *D. belizensis* are very similar to those of *D. cotinifolia* (Blunden *et al.*, 1963). The single layer of more or less rectangular endodermal cells have a suberin lamella in the walls except in the one to four passage cells opposite the protoxylem groups. In mature roots the U-shaped thickenings of the endodermal cells are lignified while the passage cells still have thin cell walls (Fig. 1B).

In the cortex of the subterranean part of adventitious shoots a periderm can be present (Fig. 4B). It is noteworthy that in these shoots, very simple, more or less collateral vascular bundles occur. The latter are very similar to those found in the seedling stem (compare Figs 5 and 6 in Von Teichman und Logischen *et al.*, 1977).

The cortex in the stem is usually about six to eight cell layers thick. The two to three layers of collenchymatous hypodermal cells are followed by chlorenchyma. Tanniferous cells and huge idioblasts occur in the cortex. The innermost cortical layer is an endodermoid layer with lignified walls, the inner tangential walls being slightly thicker.

3.3 The inner ground tissue and stele

For the sake of convenience we regard the part of the ground tissue of the tuber and cylindrical organs in which the primary vascular bundles occur, as the inner ground tissue.

3.3 (a) The inner ground tissue and vascular tissue of the tuber

In the tuber the inner ground tissue is composed of parenchyma cells with thin cellulose walls and well-developed intercellular spaces. In all the tubers examined, starch occurs only in the storage parenchyma adjacent to the vascular bundles (Fig. 4D). Hand sections showed numerous simple starch grains of different sizes and forms packed into the storage parenchyma cells. The average measurements of the larger grains are 24 μm long and 15 μm in diameter. In the tuber of *D. belizensis* the starch grains are usually simple and up to 35 μm in diameter (Blunden *et al.*, 1963). Collateral vascular bundles lie scattered throughout the inner ground tissue (Fig. 4C). Anastomosis occurs freely between the vascular bundles. These anastomosing bundles usually have one large xylem group and two phloem groups lying more or less at their abaxial pole.

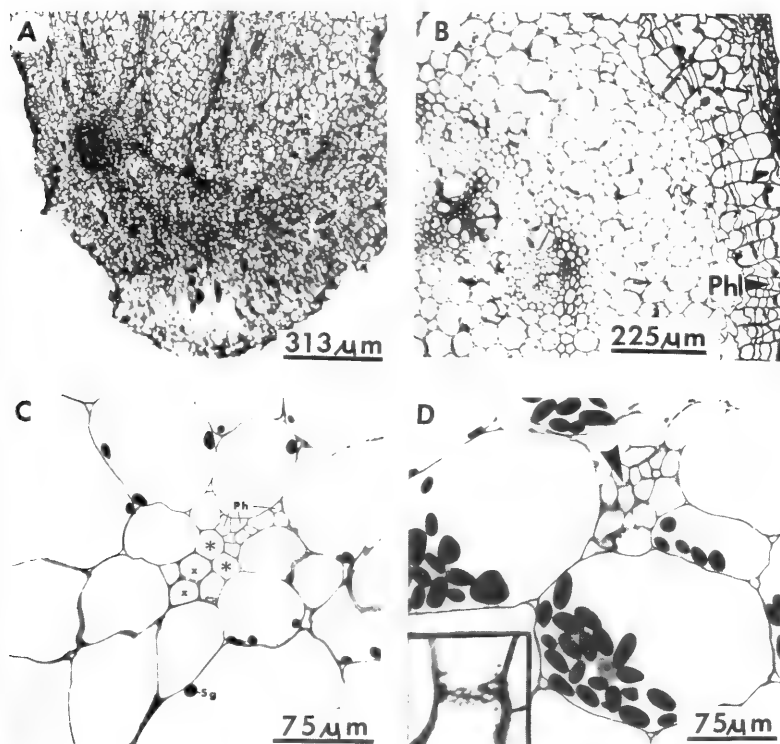


FIG. 4.

A: Longitudinal section of the tip of a very young intermediary organ showing scattered procambium strands and a young primordium; B: Transverse section of the subterranean adventitious shoot, showing the periderm, e.g. phellem (Phl), and simple vascular bundles; C & D: Transverse sections of tuber pieces, Ph—phloem unit, x—xylem; arrow in D—part of compound sieve plate, which is shown in the inset—magnification = 83 x, *—immature tracheids.

Detailed description of the vascular tissue of the tuber

During maceration the xylem elements in the cylindrical organs as well as in the roots and the shoot readily separated from the surrounding cells. When the same technique was, however, applied to the vascular bundles of the tubers, it was impossible to isolate the tracheids from the tightly adhering surrounding parenchyma and therefore no exact measurements could be made. It appears that vessel elements are absent and only tracheids are found in the tuber. The reason for the strong adherence of the surrounding cells to the tracheids is unknown.

In the tuber of *D. batatas*, *D. sinuata* and *Tamus communis* no vessels were found. However various types of tracheids occur, which also include tracheids with scalariform and reticulate thickenings (Bucherer, 1889). In *D. belizensis* the tracheids with bordered pits have a "wider diameter i.e. 21–48–87–111 μm " and are invariably longer than 500 μm (Blunden *et al.*, 1963). For *D. praezensilis* tubers Lawton and Lawton (1969) reported the presence of pitted vessels and other vessel elements varying in length and type of thickening. The tracheids are, however, more numerous than the vessels and have scalariform thickenings. According to Ayensu (1972), "of all the species investigated vessels were only found in *D. luzonensis*" tubers.

The average diameter of the large tracheids in *D. cotinifolia* tubers, as measured in transverse sections, is 24 μm , varying from 10 μm to 45 μm . The variation will henceforth be given in brackets. The estimated average length of some of the very long tracheids is 1 300 μm . Usually most of the tracheids are much shorter. According to the terminology of Esau (1965), the wall thickening in the tracheids is reticulate, scalariformly-pitted or pitted.

In the tuber (Fig. 4 D-inset) as well as in the cylindrical organs, the root and the shoot, compound sieve plates are present in the *large* metaphloem sieve tubes. Excepting the tuber, it was obvious that they occur on long oblique end walls. In *D. praezensilis* tubers, transverse, both simple and compound, i.e. oblique sieve plates occur in the narrow and wider sieve tubes respectively (Lawton and Lawton, 1969).

We agree with Koch and Bruhn (1962) that the general anatomy of the tuber (in their case *D. floribunda*) is very peculiar and differs markedly from that of the root and the shoot.

3.3 (b) *The inner ground tissue and vascular tissue of the cylindrical organ*

Even in young cylindrical organs, the inner ground tissue usually consists of storage parenchyma cells, the greater part having lignified cell walls (Fig. 2 C). Most of these cells, excepting the peripheral cells and those directly adjacent to the vascular bundle, are packed with starch grains (Fig. 2 D). The size of the starch grains varies considerably in cylindrical organs examined. This variability might be due to differences in age, time of collection and position in the plant. The average length of the starch grains is approximately 9 μm . In older cylindrical organs persisting for two or three growth seasons the whole inner ground

tissue is lignified. The collateral vascular bundles which lie scattered in this tissue (Figs 2 C & D) are very similar to those in the tuber, and anastomosis also takes place frequently.

Detailed description of the vascular tissue of the cylindrical organ

Large metaxylem vessel elements: The average length is 1 714 μm (1 337 μm –2 475 μm) and the average diameter 54 μm (30 μm –75 μm). Perforation plates mostly oblique and usually scalariform or varying to scalariform-reticulate. Short sub-apical scalariform perforation plates also occur. Vessels with a perforation plate at the one end and a blunt and pitted end at the other end, also occur. The average length of perforation plates is 169 μm (112 μm –375 μm).

Tracheids: The average length is 1 618 μm (1 200 μm –2 100 μm) and the average diameter 33 μm (15 μm –70 μm). In comparison to the root, the cylindrical organs have relatively many tracheids. Their ends are often forked.

Fibres: The average length of the relatively few fibres that occur is 543 μm (375 μm –600 μm) and the average diameter is 13 μm (9 μm –18 μm).

Sieve tubes: The average diameter of the largest metaphloem sieve tubes as measured in transverse sections is 22.3 μm (9 μm –45 μm).

The pits in the large metaxylem vessels and tracheids of the cylindrical organs, the root and the shoot are bordered, and vary from scalariform, to mostly oval alternate or round alternate and sometimes opposite.

3.3 (c) *The stele of the root*

In the root a two to five layered pericycle is found. The cells bordering on the phloem have thickened lignified cell walls. The polyarch stele varies from 10-arch to 20-arch. The stele sometimes comprises up to two-thirds of the root diameter. The huge xylem vessels lie scattered in the pith, where idioblasts also occur (Fig. 1 A & B).

Detailed description of the vascular tissue of the root

Large metaxylem vessel elements: The average length is 3 795 μm (1 350 μm –7 200 μm) and the average diameter 83 μm (30 μm –120 μm). Perforation plates usually oblique and mostly scalariform to scalariform-reticulate. Their average length is 124 μm (30 μm –510 μm). Concave, relatively short perforation plates were also observed.

The widest vessels in *D. belizensis* have a diameter of "45–105–144–159 μm " (Blunden *et al.*, 1963). The average length and diameter of vessels in *D. sansibarensis* is "1 191 μm (range 820–5 000 μm) and 65 μm (range 24–180 μm) respectively. Pits on lateral walls alternate and opposite. Perforated scalariform plates mostly oblique, few horizontal. End plates 256 μm long (range 84–1 080

μm)” (Tan and Rao, 1974). The end plates in *D. sansibarensis* are also usually scalariform, or scalariform to reticulate (Tan and Rao, 1974).

Tracheids: The average length of the relatively few tracheids in the root of *D. cotinifolia* is 2 980 μm (2 260 μm –4 275 μm) and the average diameter 26 μm (15 μm –53 μm).

Fibres: The average length is 533 μm (337 μm –750 μm) and the average diameter 9 μm (7 μm –13,5 μm).

Sieve tubes: The average diameter is 49,6 μm (21 μm –75 μm). The sieve tube diameter in the case of *D. belizensis* is 15 to 36 μm (Blunden *et al.*, 1963).

3.3 (d) *The stele of the shoot*

In the internode a six to eight layered mechanical tissue of thick-walled lignified parenchyma ensheathes the central cylinder. The ground tissue between the vascular bundles is parenchymatous. Idioblasts and tanniferous cells occur in the ground tissue and pith. One, or up to three common vascular bundles lie in alternation with the large cauline vascular bundles. The type of common vascular bundle which is usually present was described precisely by Ayensu (1972), namely “a V-shaped arrangement of metaxylem vessels and tracheids together with at least 2 phloem units terminating the flanges of the V, and a third phloem unit at the converging ends of the V,” (Fig. 1 C). Apart from this “typical” type, atypical bundles were found in six of the internodes examined, where only *one* phloem unit occurs between the flanges of the V, while one large metaxylem vessel occurs at the base of the V (Fig. 1 C). Slight variations, other than this, were noticed in a few internodes.

The cauline vascular bundle which is present in all internodes examined, has *two* large phloem units on the inner side of the two large metaxylem vessels (Fig. 1 C). In this bundle a third phloem unit occurs at the abaxial side of the elliptical arrangement of metaxylem vessels and tracheids. The second most common type has four phloem units, three of these correspond to those described above and the fourth unit occurs just to the outside of and slightly between the two large metaxylem vessels (Fig. 2 B). In only two of the ten internodes examined a few cauline vascular bundles with two phloem units occur, namely *one* to the inside of the two large metaxylem vessels and one at the periphery. This bundle type was described by Ayensu (1972) for *D. cotinifolia*.

Detailed description of the vascular tissue of the shoot

Metaxylem vessel elements:

Although the internodal stem pieces used for maceration were up to 40 mm long, the ends of most vessel members were still cut off at one end. The longest metaxylem vessel element measured was 28 800 + μm . The shortest being 8 100 + μm , the approximate average length is 18 180 μm and the average diameter 131,6 μm (50 μm –240 μm).

In comparison Ayensu (1972) found the average diameter of the large vessels of *D. cotinifolia* to be 98 μm . Shah *et al.* (1967) described the internodal vessel elements of *D. alata*. These elements also vary greatly in size, the length of elements with foraminate perforations range from about 218 μm to 1 650 μm and the diameter from 13 to 16 μm ; while elements with scalariform perforations vary from 1 000 to 7 700 μm in length and their diameter from 23 to 115 μm and those with reticulate perforations from 450 to 4 050 μm and 13 to 113 μm respectively.

Tan and Rao (1974) measured the diameter of the largest vessel in the internode of *D. sansibarensis* as 882 μm . In *Tamus communis*, *D. batatas* and *D. sinuata* scalariform perforation plates also occur on oblique end walls in the stem metaxylem elements. These elements also have linearly bordered pits in an alternate arrangement (Bucherer, 1889). The perforation plates of the large metaxylem elements of *D. cotinifolia* usually occur on long oblique end walls and are scalariform, mostly scalariform-reticulate and sometimes reticulate. Concave and even convex perforation plates also occur. The average length is 956 μm (210 μm to 3 000 μm). The number of cross bars in scalariform plates varies greatly and up to 144 cross bars per plate were observed.

Tracheids: Tracheids with annular, helical, reticulate and scalariform thickenings occur. Scalariformly-pitted, as well as pitted tracheids are also present. The approximate average length of the scalariformly-pitted tracheids is 1 298 μm (300 μm —2 400 μm). The average diameter of these is 16 μm (12 μm —23 μm). The shorter tracheids usually have bizarre shapes. Their length measures approximately 300 μm , and they usually have an alternate pitting. They were already described by Bucherer (1889) for the tuber of *Tamus communis*.

Fibres: The average length is 756 μm (390 μm —1 110 μm) and the average diameter 10 μm (7.5 μm —15 μm). Probably more fibres occur in the shoot than in the other organs. They appear to be concentrated around the phloem units (Fig. 2B). The pits in the end walls of some fibres are so closely spaced that they create the impression of a pitted plate.

Sieve tubes: In the cauline vascular bundles, on the inside of the two large metaxylem vessels, were measured in transverse sections. The average diameter of these sieve tubes in shoots with a relatively small diameter is 53 μm (30 μm —75 μm), while in shoots with a relatively large diameter it is 86.5 μm (60 μm —112.5 μm). In comparison Ayensu (1972) found the average diameter of the large sieve tubes of *D. cotinifolia* to be 28 μm .

Tan and Rao (1974) also found a definite correlation between stem diameter and vessel diameter in *D. sansibarensis*.

IV. CONCLUSIONS

Although the anatomy of the intermediary organs, i.e. the tubers and cylindrical organs, of *D. cotinifolia* Kunth seems to be unique, there is a characteris-

tic which reminds one of roots, i.e. the piliferous layer. Characteristics which are similar to those of the seedling stem and subterranean part of adventitious shoots are: (1) the type of vascular bundle; and (2) the presence of a phellem.

The type of perforation plate in the large metaxylem vessel elements, the pitting of these elements and the tracheids of the cylindrical intermediary organs are similar to that of the root and shoot. These long scalariform perforation plates on the oblique end walls are considered to be primitive (Wagner, 1977). The intermediary organs, the root and the shoot have compound sieve plates on oblique end walls in the large metaphloem sieve tubes. The average diameter of the sieve tubes in the intermediary organs is about half that of the sieve tubes of the root and shoot. According to Cheadle (1948) sieve tubes with compound sieve plates are primitive. He also mentions that this type of sieve tube does not occur in the bulbs and corms of the monocotyledons.

That vessels are absent in the tubers and that the tracheids are ensheathed by strongly adhering parenchyma cells are unique features of these organs.

The intermediary organs are unique in the following respects: (1) the presence of a second lateral meristem or meristematic zone in the outer ground tissue; (2) in that the latter gives rise to secondary vascular tissue, ground tissue and endogenous primordia; (3) these primordia enable these organs to serve as vegetative reproductive organs, besides being storage organs; (4) the arrangement of the vascular tissue in scattered bundles, and (5) due to their origin from the hypocotyl, the tips of the very young intermediary organs resemble neither a root nor a shoot apex.

It remains to be mentioned, that the metaxylem vessel elements in *D. cotinifolia* shoots seem to be longer ($28\ 800 + \mu\text{m}$) than any previously described elements in *Dioscorea* spp.

The general anatomy of the intermediary organs is slightly similar to that of the *Dioscorea* rhizomes described by Ayensu (1972).

Some anatomical characters of the shoot of *D. cotinifolia*, i.e. (1) the rather bizarre shaped tracheids with alternate pitting and (2) the alternate pitting and scalariform perforation plates in the large vessels, are very similar to those of the stem of *Stemona tuberosa* Lour. (Govindarajulu and Rajasekaran, 1972).

All these interesting features are indications of a probable relationship between the Dioscoreaceae and the genus *Stemona* of the Stemonaceae (Roxburghiaceae) mentioned by Ayensu (1972).

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**STUDIES OF SEED GERMINATION AND SEEDLING COMPETITION IN
VIRGILIA OROBOIDES (BERG.) SALTER, *ALBIZIA LOPHANTHA* (WILLD.)
BENTH. AND *ACACIA LONGIFOLIA* (ANDR.) WILLD.**

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ABSTRACT

A pilot ecological study comparing the indigenous legume tree *Virgilia oroboides* with two ecologically similar aliens, *Albizia lophantha* and *Acacia longifolia*, was initiated. Similarities were found in seed germination biology, with all three species showing rapid germination once seed dormancy is broken. Differential inhibition of seed germination with leaf litter and inter-specific seed-mix treatments was investigated and showed increasing sensitivity in the order *Virgilia*, *Albizia*, *Acacia*. A semi-natural replacement series interspecific seedling competition experiment revealed that all three species occupy similar niches. The order of aggressiveness was found to be *Virgilia*, *Albizia* then *Acacia*, the interaction effects being most clearly observed in the root biomass. Species seed-mass and energy-content were compared. Shoot and root increments relative to final shoot and root biomasses were also examined, in addition to the performance of each species in nutrient and non-nutrient media. All findings, together with further sundry observations, including *in vivo* seed and seedling predation measurements, were incorporated into the competition situation. Conclusions were that success of a particular species in a given combination of species depends on a large number of factors, e.g. varying nutrient and moisture availabilities of different soils, as well as differential predation on species. It is suggested that if the environment is manipulated correctly *Virgilia* (or other suitable indigenous species) could possibly be used as a subsidiary control measure against the invasive aliens *Albizia* and *Acacia*.

UITTREKSEL

STUDIES IN SAAD ONTKIEMING EN SAAILING KOMPETISIE BY *VIRGILIA OROBOIDES* (BERG.) SALTER, *ALBIZIA LOPHANTHA* (WILLD.) BENTH. EN *ACACIA LONGIFOLIA* (ANDR.) WILLD.

'n Loods ekologiese ondersoek om die inheemse peulplant boom *Virgilia oroboides* te vergelyk met twee ekologiese vergelykbare uitheemses, *Albizia lophantha* en *Acacia longifolia* is begin. Ooreenkomste met die saad ontkiemingsbiologie, waar al drie vinnig ontkiem na die verbreking van die rus. Differensiase met die onderdrukking van saad ontkieming met die blare met tussensoorte mengels wat ondersoek is, dui op 'n toename in sensitiviteit in die volgorde *Virgilia*, *Albizia*, *Acacia*. 'n Half-natuurlike vervangings reeks intersoort-kompetisie proef dui daarop dat al drie in vergelykbare posisies groei. Die volgorde van aggressiewiteit wat gevind is was *Virgilia*, *Albizia* en *Acacia* waar die interaksie effek die duidelikste uit die wortelbiomassa blyk. Loot en wortelgroei relatief tot die finale loot en wortelbiomassa was ondersoek en die groei van elke soort in 'n voedings en voedingslose media vergelyk. Alle bevindings, saam met verdere opmerkings insluitende *in vivo* saad en kiemplant benuttig meetings, word saamgevoeg in die kompeti-

sie situasie. Gevolgtrekkings dat die sukses van 'n bepaalde soort in 'n gegewe kombinasie van soorte afhang van 'n groot aantal faktore soos wisselende voedings en vogtigheid beskikbaarheid in verskillende gronde sowel as gedifferensieerde vreet op die soorte. Dit word voorgestel dat as die omgewing reg manipuleer word *Virgilia* (of 'n ander geskikte inheemse soort) moontlik gebruik kan word as 'n bykomende beheer maatreël teen die uitheemse *Albizia* en *Acacia* wat natuurlike veld inneem.

INTRODUCTION

Both *Albizia lophantha* and *Acacia longifolia* are invasive woody plants of Australian origin in the south-western Cape (Stirton, 1978). *Virgilia oroboides*, a southern and south-western Cape endemic (Coates Palgrave, 1977), is probably the nearest indigenous ecological analog of *A. lophantha* and *A. longifolia*. All three species occupy very similar habitats and have similar characteristics as indicated below:

1. All grow on moist, relatively fertile, south- and east-facing mountain slopes with similar altitudinal ranges.
2. All are nodulated legumes.
3. All are seed-regenerating species that grow from long-lived, hard-coated, pyrophytic seed which accumulate in the soil. None of the species coppice after fire.
4. Unlike most indigenous trees *Virgilia* has a very fast growth rate of up to 2 to 3 m per annum (Phillips, 1926), which is comparable with the rapid growth rates of the two introduced species.

Thus the broad hypothesis that *Virgilia* could, if environmental conditions were manipulated correctly, be given a competitive advantage over one or both of the two invasive Australian plants, was proposed and a pilot experimental study emphasizing interspecific interaction between all three species was conducted. The specific aims of the study were:

1. To compare the germination rates and percentages of each species (germinated alone), with the rates achieved on intra- and interspecific leaf litter mixtures, and in interspecific seed mixtures.
2. To compare energy contents of seeds of each species and to correlate the results with short-term, controlled interspecific seedling competition experiments.
3. To compare the rates of seedling shoot and root growth between species in soil, and in vermiculite with and without nutrients.
4. To make observations on the relative seed and seedling predation for each species in nature.

Seed and leaf-litter for these studies was collected in early summer of 1979 from Constantia Nek, Cape Province.

MAXIMUM SEED GERMINATION RATES

Seed germination tests

It has been demonstrated that poor germination responses in the three species are due principally to the impermeability of the testa to water (Phillips, 1926; Clements *et al.*, 1977). So all seeds were individually chipped at their micropylar ends to ensure the fastest possible germination response.

To investigate interspecific effects three replicate batches consisting of 50 seeds for each species, and in 1:1 ratios with each other, were placed in 50 mm petri dishes containing two No. 1 Whatman filter papers.

In the "leaf-litter" treatments the filter papers were inserted between 4 g of freshly ground leaf litter and the seeds. In order to prevent fungal infection the procedure given by Clemens *et al.* (1977) was followed.

All germination and incubation experiments were conducted at 27 °C (± 1 °C). Relative humidity was controlled at 100 %, and daylength adjusted to a constant 12-hour period at an intensity of 40 000 lux. Adequate moisture conditions were maintained in each dish and counts of germinated seeds (i.e. seed with emerged radicle length greater than 1 mm) were made daily over a period of 14 days. Germinated seeds were not removed for the duration of the test period.

The mean daily percentage germinations were arc-sine transformed to make them suitable for the analysis of variance (Sokal and Rohlf, 1969). Initially both the rates and final germination percentages for pure seeds of each species were compared with one another visually at the 95 % confidence limit. The number of days taken for half the sample to germinate (mean day) was also calculated for each species, together with the standard deviation. Separate comparisons were then made between the arc-sine transformed data for daily germination of pure seeds, seeds on litter, and seed-mixes for each species. As the daily germination rates of the treated seeds and the standards (pure seeds) were compared individually, a series of standard *t* tests was applied to determine whether the differences were significant.

Results

Germination was quick and decisive with no changes in percentage germination beyond day five. The germination rates of standards were similar for all species (Figure 1). The time taken for half the seeds of each species to germinate was 0.8; 0.8 and 1.5 days for *Virgilia*, *Albizia* and *Acacia* respectively.

Discussion

Virgilia seeds showed relatively low inhibition of germination in all treatments (Figure 2a). Only on the first and second days on *Albizia* litter, and on the first day on *Acacia* litter, was there a significant reduction of germination rate compared with the pure seed standard (Table 1).

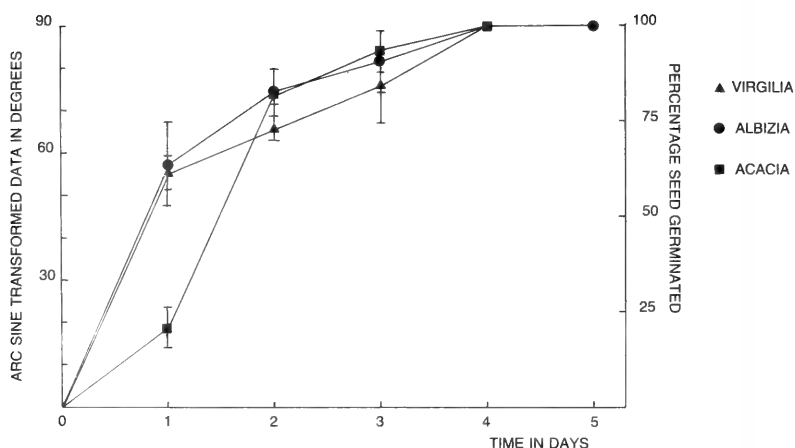


FIG. 1.
Germination rates of seeds (95 % confidence limits shown)

Albizia seeds showed greater sensitivity than *Virgilia* seeds to the leaf litter and seed-mix treatments (Figure 2b). Inhibition of germination was most pronounced with the leaf-litter treatments, being greatest on its own and on *Virgilia* litter, and showing significant inhibition from day 3 onwards on *Acacia* litter. The actual rates of germination were significantly reduced in the seed-mix treatments only from day 1 to day 3 with *Virgilia* seeds, and only for day 1 with *Acacia* seeds (Table 1).

Of all the species *Acacia* exhibited greatest inhibition. With the exception of the *Albizia* mix all other treatments produced marked inhibition of both the rates, and the overall final germination of the *Acacia* seed (Figure 2c, Table 1).

Of interest was the fact that the litter of the parent species caused greater inhibition to the germination of both *Acacia* and *Albizia* and appeared insignificant in *Virgilia* (Figures 2a, b, c, Table 1).

SEEDLING COMPETITION STUDIES

Assessment of seed mass, energy content and moisture content

Fifty seeds of each species were each weighed then dehydrated whole at 65°C for seven days and re-weighed. These seeds were then finely ground and dehydrated for a further three days and re-weighed again. It was, therefore, possible to compare resistance of each species to dehydration through the seed-coat with its overall moisture content. The calorific value of 2 g sub-samples of each dried sample was then obtained by means of bomb calorimetry.

TABLE 1.
Germination rates in days of treated seeds compared with pure standards ($t^{0.05} = 2.776$).

Treatment	VIRGILIA				ALBIZIA				ACACIA			
	1	2	3	4	1	2	3	4	1	2	3	4
On VIRGILIA litter	1.01	0.03	0.20	2.02	[>5]	>5	>5	>5	[3.05]	>5	>5	>5
On ALBIZIA litter	[>5]	[>5]	2.34	1.76	[>5]	>5	>5	>5	[>5]	>5	>5	>5
On ACACIA litter	[4.63]	2.69	1.58	1.93	[>5]	2.16	3.40	>5	[2.79]	>5	>5	>5
With VIRGILIA seeds	—	—	—	—	[3.57]	2.83	[2.90]	1.38	[>5]	>5	>5	5.34
With ALBIZIA seeds	1.85	0.75	0.36	2.02	—	—	—	—	1.52	0.26	0.20	—
With ACACIA seeds	1.47	3.65	0.34	2.01	[3.39]	0.12	0.32	0.30	—	—	—	—

[] Indicates period of inhibition

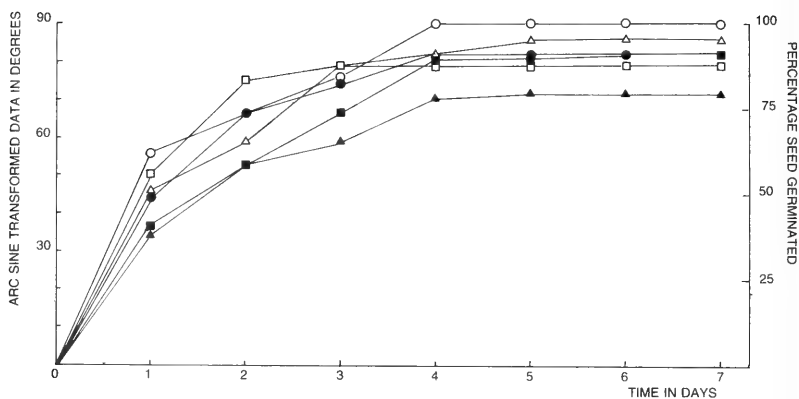


FIG. 2a.
Germination rates of *Virgilia*.

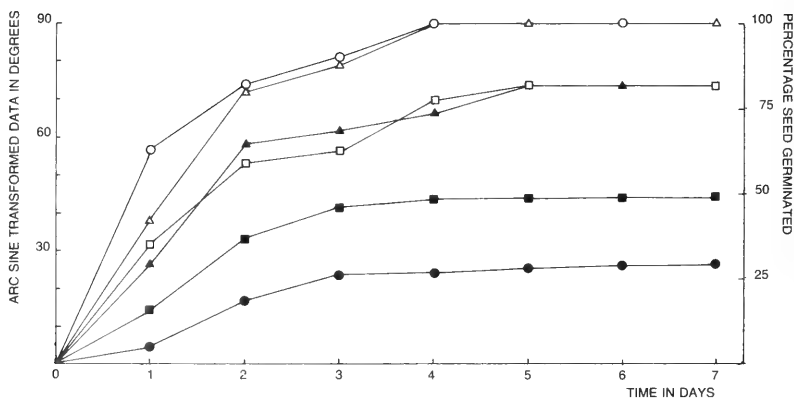


FIG. 2b.
Germination rates of *Albizia*.

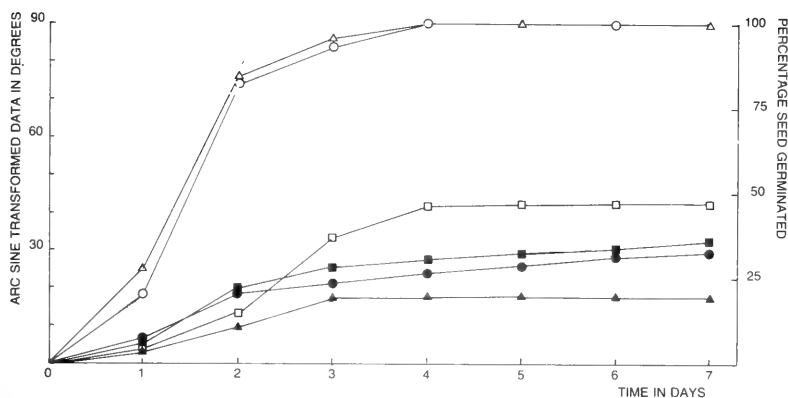


FIG. 2c.
Germination rates of *Acacia*.

Key to Fig. 2a, b, c

- Species I (J, K) plain.
- △ Species I (J, K) with seeds of species J (K, I)
- Species I (J, K) with seeds of species K (I, J)
- Species I (J, K) on litter of species I (J, K)
- ▲ Species I (J, K) on litter of species J (K, L)
- Species I (J, K) on litter of species K (I, J)
- I = *Virgilia oroboides*
- J = *Albizia lophantha*
- K = *Acacia longifolia*

Discussion

The individual seed weights showed a very low standard deviation; *Albizia* produced the heaviest seeds, followed closely by *Virgilia*, with *Acacia* having the lightest seeds.

A modified *t* test for small sample size, the Lord's Range test (Sokal and Rohlf, 1969) showed that individual seed energies were significantly different at $L^{0.05}$ for *Albizia* and *Virgilia*, and also at $L^{0.01}$ for *Acacia* compared with *Virgilia* and for *Acacia* compared with *Albizia*. The seed energy/undried seed mass ratios showed the same order of magnitude as the individual undried seed mass. However, the ratio for *Acacia* was lower than that of both the other species. This means that, relative to the other species, even less energy is present in the *Acacia* seed than is apparent from the undried mass.

TABLE 2.
Comparison between seed mass, seed moisture content and seed energy content for *Virgilia*, *Albizia*, and *Acacia*
($L\ 0.05 = 1.71/L\ 0.01 = 3.96$)

Species	Mass of seed 9	Percentage moisture loss after whole seed desicca- tion at 65 °C for 7 days	Total percentages moisture	Sub-sample batch number for energy determina- tion	Energy per gram of dried seed KJ	Energy per gram of un- dried seed KJ	Energy per seed KJ	L values between species for seed energies
<i>VIRGILIA</i>	0.07858 ± 0.00004	91.31	7.02	1 2 Mean	21.283 21.861 21.572		1.5550 1.5972 1.5761	<i>VIRGILIA</i> vs. <i>ALBIZIA</i> 1.772
<i>ALBIZIA</i>	0.09255 ± 0.00005	67.61	7.75	1 2 Mean	20.650 21.682 21.166		1.7630 1.8511 1.8078	<i>ALBIZIA</i> vs. <i>ACACIA</i> 16.449
<i>ACACIA</i>	0.016650 ± 0.000007	62.22	8.92	1 2 Mean	18.008 18.341 18.175		0.2731 0.2781 0.2756	<i>ACACIA</i> vs. <i>VIRGILIA</i> 27.553

Of all the test species *Virgilia*, when dehydrated whole, showed the highest percentage of overall moisture content lost through its seed-coat. This presumably indicates a higher seed-coat permeability.

Seedling competition using the replacement series technique

Freshly germinated seed of *Virgilia*, *Albizia* and *Acacia* were sown in pure cultures, as well as in 1:1 mixtures with species individuals set alternately to one another. Fallen seed of *Virgilia* may be found in natural concentrations of up to 0.2 seeds per cm² (Phillips, 1926), whereas that of *Acacia* can be found at concentrations of up to 3 seeds per cm² (Milton, 1980). Germinated seed were set at concentrations of 1 per cm² in 7 × 7 matrices (with the omission of plantings at the 49th position, allowing equal numbers per species). Two replicate matrices were prepared for both pure and mixed cultures. The rich loam soil used for the experiment was taken from the A horizon at a site in the Kirstenbosch National Botanic Gardens, where all three test species are known to grow vigorously.

The experiment was conducted outside during late autumn and winter, a cool wet period in the south-western Cape when natural germination in the field had been observed. Precautions were taken against predation, and a transparent (95 % light transmission) corrugated fibre-glass sheet was suspended 1 m above the seedling containers to permit controlled watering.

After twelve weeks the seedlings were harvested, cleaned and then dried at 80 °C. The total dry-mass measurements for shoot and root biomasses were taken separately for each species from each culture, and representative examples were photocopied for visual comparison (Figures 3b, 4b and 5b).

Analysis of data

The "replacement series" approach is an experimental design devised by de Wit (1960) to measure the effects of one species on the other in species combinations grown in mixtures. This approach adopts as a standard for comparison the pure stands of each species grown at the same densities as the mixtures, thus allowing all conclusions to be determined on a proportional and therefore relative basis. Results are represented pictorially by means of "replacement series" curves for each species combination. This procedure was followed with the data from the present experiment (Figures 3a, 4a and 5a).

In addition the data were analysed to determine certain important features concerning species interactions. In order to determine whether each test species possesses ecological niche overlap with the others (i.e. whether there is competition for common limiting resources), the "Relative Yield Totals" (RYT) for each of the interacting species pairs were calculated. The sum of the relative yields of species "I" grown in mixtures with species "J" (R_I) and of species J

grown in mixtures with species "I" (R_I) is equivalent to the RYT for the two species. Here

$$R_I = \frac{M_I}{P_I} \text{ and } R_J = \frac{M_J}{P_J}$$

where $M_{I(J)}$ = yield of species $I(J)$ in mixture, and $P_{I(J)}$ = yield of species $I(J)$ in a pure stand. If the RYT values are equal to unity this indicates that the mixed species pairs fill the identical ecological "space" (Harper, 1977). In order to determine the statistical significance of the conclusions inferred by the RYT values, the actual yield of each mixture was compared with the sum of half the actual yields of the two corresponding pure cultures, following the method of Burdon and Pryor (1975). The "Lord's Range test" was used to test whether the species in mixtures were occupying the same ecological niche.

Even if it is found that the species occupy sufficiently similar ecological niches to allow direct competition for resources, this factor gives no information about the significance of relative enhancement/inhibition effects produced by the mixing. Thus inferences drawn from the shapes of the "replacement series" curves (convexity illustrating enhancement and concavity inhibition) were tested. Lord's Range values were thus calculated to see whether the difference was significant between relative yields for the replicate pairs of each species and the corresponding pairs of "expected" relative yields. The "expected" relative yield is defined as being half the value of the calculated RYT for each replicate.

In order to extend the conclusions concerning the effects of the test species interactions, similar "relative yield" analyses were completed for both shoots and roots separately. Actual shoot-root yield borderlines were also depicted on the "replacement series" diagrams.

Results and discussion

All RYT values (which are marked on Figures 3a, 4a, 5a) were found to be close to unity, thus providing a rough indication that the test species fill very similar ecological niches to one another. Comparisons of the actual yields for each mixture with the sum of half the actual yields of the corresponding pure cultures produced values which were all insignificant at $L^{0.05}$. This means that one must accept the null hypothesis that the species are competing with one another for the same ecological space, which agrees with the conclusions obtained from the RYT values. Inspection of the L values (Table 3) gives an indication of the ecological relationships between the species as regards competition for the same resources. The order of increasing ecological "relatedness" appears to be as follows: *Virgilia-Acacia*, *Virgilia-Albizia* and lastly, *Albizia-Acacia*.

TABLE 3.
Competition between species and effects of interaction in mixture: L values ($L_{0.05} = 1.71$ and $L_{0.01} = 3.96$)

Species Pair	Yield mixed vs. $\frac{1}{2}$ Yield pure	Relative Yield Total (RYT)	Species	Total Plants RY vs. $\frac{1}{2}$ RYT	Shoots alone RY, vs. $\frac{1}{2}$ RYT _r	Roots alone RY, vs. $\frac{1}{2}$ RYT _r
<i>VIRGILIA</i> vs. <i>ALBIZIA</i>	1.3482	1.0583	<i>VIRGILIA</i>	1.1531	0.6014	5.6933 (S)
			<i>ALBIZIA</i>	2.2288 (S)	0.9954	3.4247 (S)
<i>ALBIZIA</i> vs. <i>ACACIA</i>	0.6306	1.0795	<i>ALBIZIA</i>	2.4430 (S)	1.0771	4.0856 (S)
			<i>ACACIA</i>	1.8460 (S)	1.4703	2.7188 (S)
<i>ACACIA</i> vs. <i>VIRGILIA</i>	1.5952	0.9882	<i>ACACIA</i>	2.3828 (S)	1.3713	5.3327 (S)
			<i>VIRGILIA</i>	0.8429	0.8429	2.3150 (S)

The replacement series curves indicate fairly marked enhancement/inhibition effects between the various competing species pairs (Figures 3a, 4a, 5a). The Lord's Range comparisons of the relative yields and $\frac{1}{2}$ RYT's revealed significance at the 95 % level for all competitors, with the exception of *Virgilia* (Table 3). However, it must be emphasized that both *Albizia* and *Acacia* show significant inhibition in biomass increment in the presence of *Virgilia*.

Finally, *Albizia* is significantly enhanced and *Acacia* significantly depressed when in mixture.

The comparisons between expected relative yield and observed relative yields, calculated for shoots and roots separately, show very definite differences between the respective *L* values (Table 3). It is clear that differences in the observed relative yields of *shoots* alone, for all the species pairs, is insignificant at the 95 % confidence level. That most competitive enhancement/inhibition effects are manifest in the root relative yields is clearly indicated by the much higher *L* values. Root relative yields show significant differences from the expected values for all species in all combinations with some *L* values even exceeding the 99 % confidence levels: *Virgilia* is enhanced when in mixture with *Albizia*; *Acacia* is inhibited when in mixture with *Virgilia* and *Albizia* is enhanced when in mixture with *Acacia*. Some of the general competition effects for each species are apparent in Figures 3b, 4b and 5b.

In summary, the test species appear to occupy very similar niches with competition being, therefore, direct, and with the interaction effects being most significant in the roots.

EARLY SHOOT AND ROOT GROWTH RATES

A comparison between the shoot and root growth rates of seedlings in soil

Seedlings of *Virgilia*, *Albizia* and *Acacia* were grown in specially constructed root chambers (Gerard, 1978), set at 45° to the vertical, and root elongation was recorded at fortnightly intervals. The soil used and the environmental conditions for growth were the same as those employed in the seedling competition experiment. Marked root growth increments were later measured by means of an opisometer.

Simultaneously with the recording of root increments measurements of shoot heights were also taken for each plant.

At the end of 9 weeks the seedlings were harvested, cleaned and photographed in order to determine approximately what proportion of the roots had been visible through the transparent perspex sides of the chambers while growth was being monitored. Finally the seedlings were oven dried at 80°C and weighed.

Results and discussion

Cumulative shoot and root increments were compared between species for

RYT for 0.5/0.5 mixture = 1.056

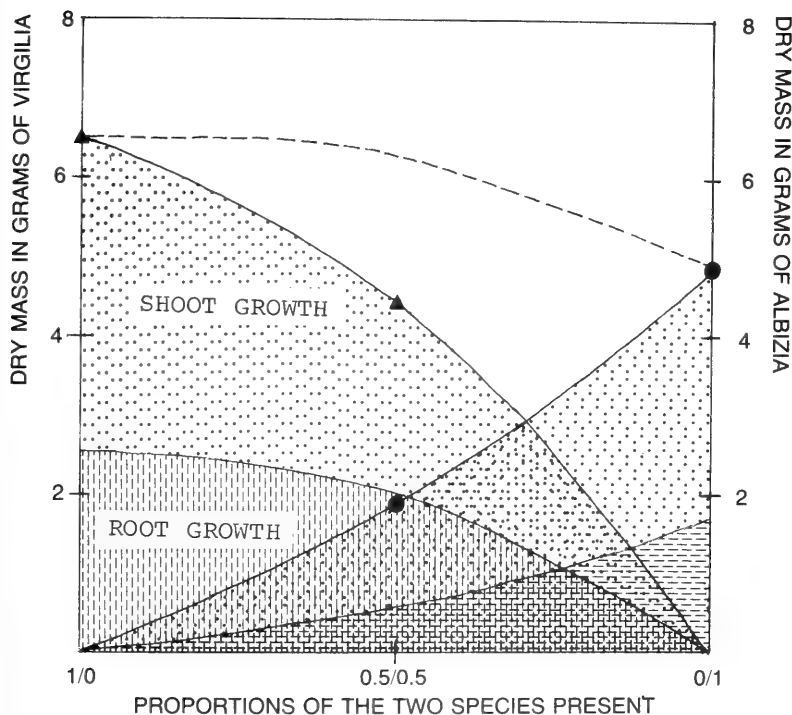


FIG. 3a.

A "replacement" series diagram of *Virgilia* = ▲ vs. *Albizia* = ●.

each time interval using a series of one-way Anova variance tests (Sokal and Rohlf, 1969). If the null hypothesis for these tests was rejected the Tukey's method of multiple comparisons (Zar, 1974) was applied to test significance between individual species combinations. It was thus possible to determine if and when seedlings of each species showed significantly different root and shoot growth rates from one another. A similar analysis was also performed to test differences between the final mean dry weights for each species.

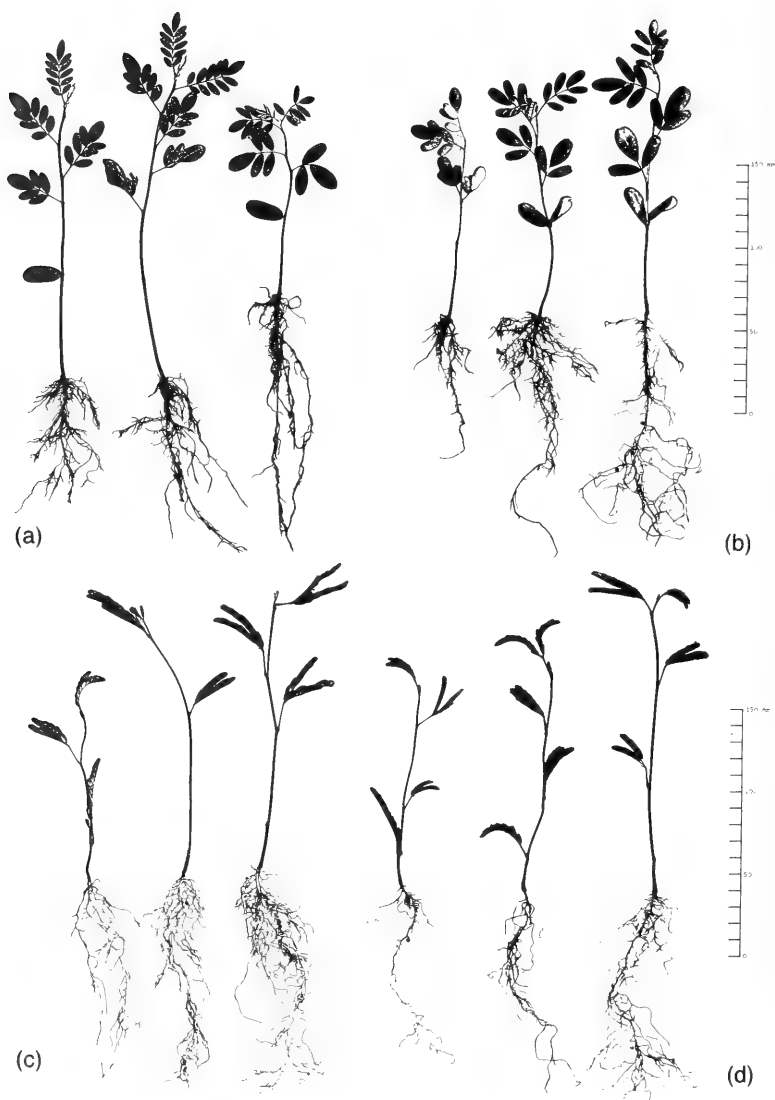


FIG. 3b.

Seedlings selected at random from pure and mixed stands by *Virgilia*, *Albizia*—showing effects of interaction.

- (a) 'Pure' *Virgilia* (b) 'Mixed' *Virgilia*—slightly enhanced root development
 (c) 'Pure' *Albizia* (d) 'Mixed' *Albizia*—slightly reduced root development

RYT for 0.5/0.5 mixture = 1.082

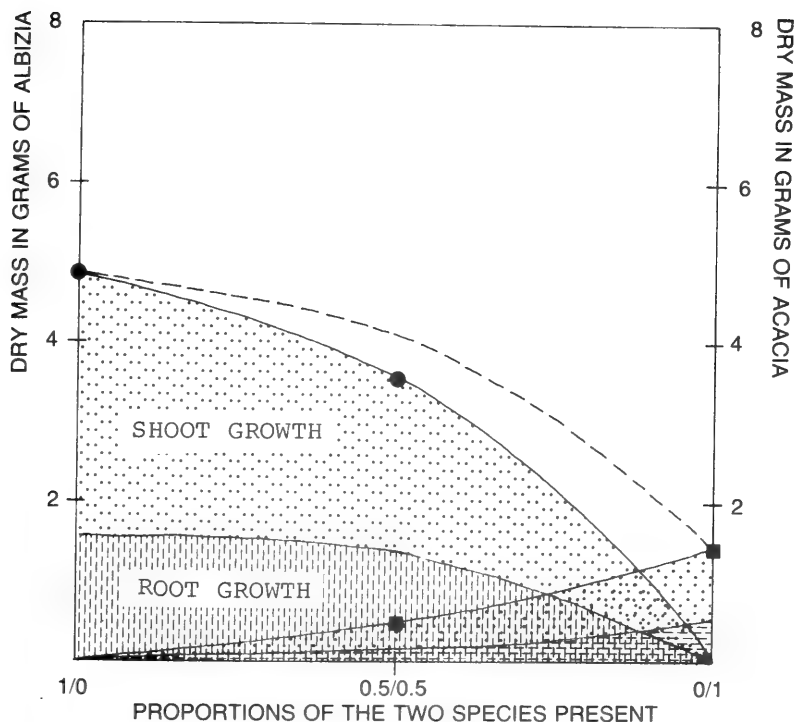


FIG. 4a.

A "replacement" series diagram of *Albizia* = ● vs. *Acacia* = ■.

In addition, certain proportions, together with standard deviations, concerning shoots and roots, were calculated and comparisons made. These were, firstly, final root/shoot length and root/shoot dry-weight proportions and secondly, final shoot weight/shoot length and root weight/root length proportions.

Visual comparison between the photocopied seedling roots (Figure 6c) and the transparent sheets whereon root growth increments had been traced, showed that a considerable part of the root length had been visible during the monitoring procedure.

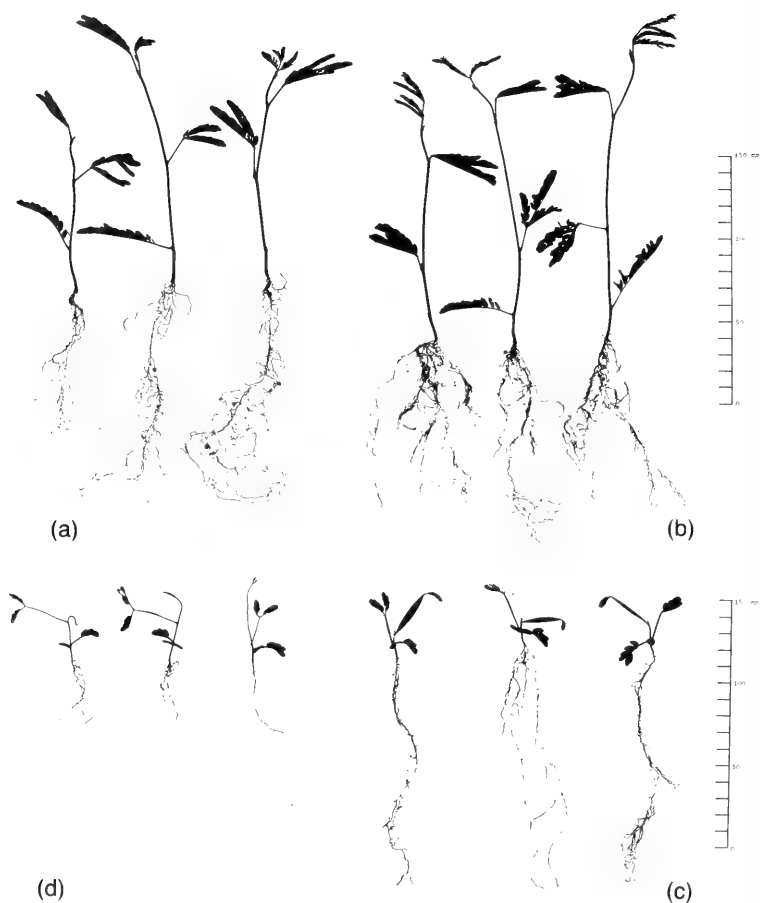


FIG. 4b

Seedlings selected at random from pure and mixed stands of *Albizia*, *Acacia*—showing effects of interaction.

- (a) 'Pure' *Albizia*
- (b) 'Mixed' *Albizia*—slightly enhanced root development
- (c) 'Pure' *Acacia*
- (d) 'Mixed' *Acacia*—reduced root development and etiolated stems and leaves

RYT for 0.5/0.5 mixture = 0.986

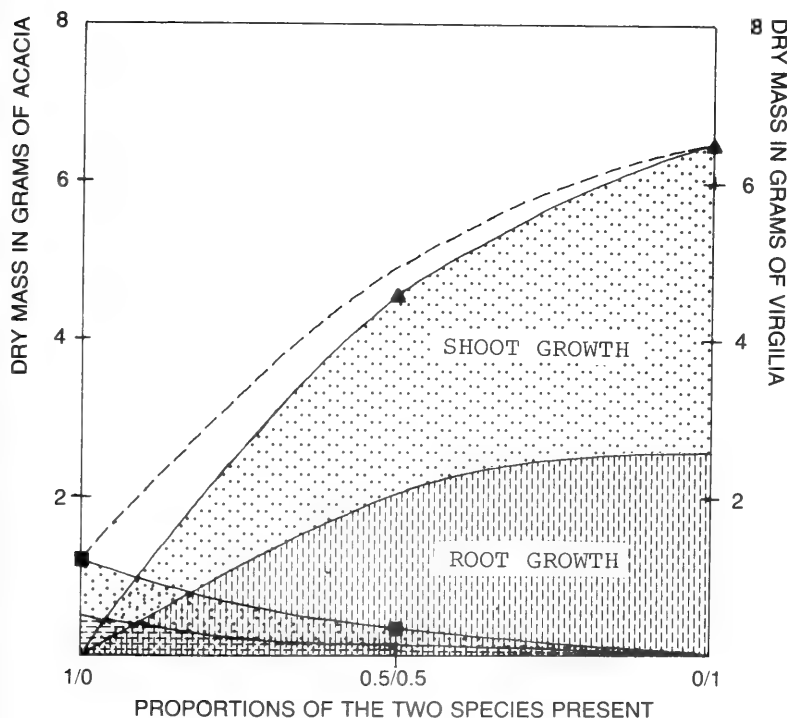


FIG. 5a.

A "replacement" series diagram of *Acacia* = ■ vs. *Virgilia* = ▲.

The comparison of rates of shoot increment showed significant differences between species throughout (Table 4a). From the curves in Figure 6a it can be noted that the rates of growth for all species appear most rapid over the first two weeks, probably as a result of the initial seed energy content. Although *Virgilia* shows a significantly greater shoot length increment than *Albizia* from week 4 onwards, *Albizia* appears to possess a slightly faster rate of growth than *Virgilia*, possibly indicating that the former could eventually out-compete the latter. A

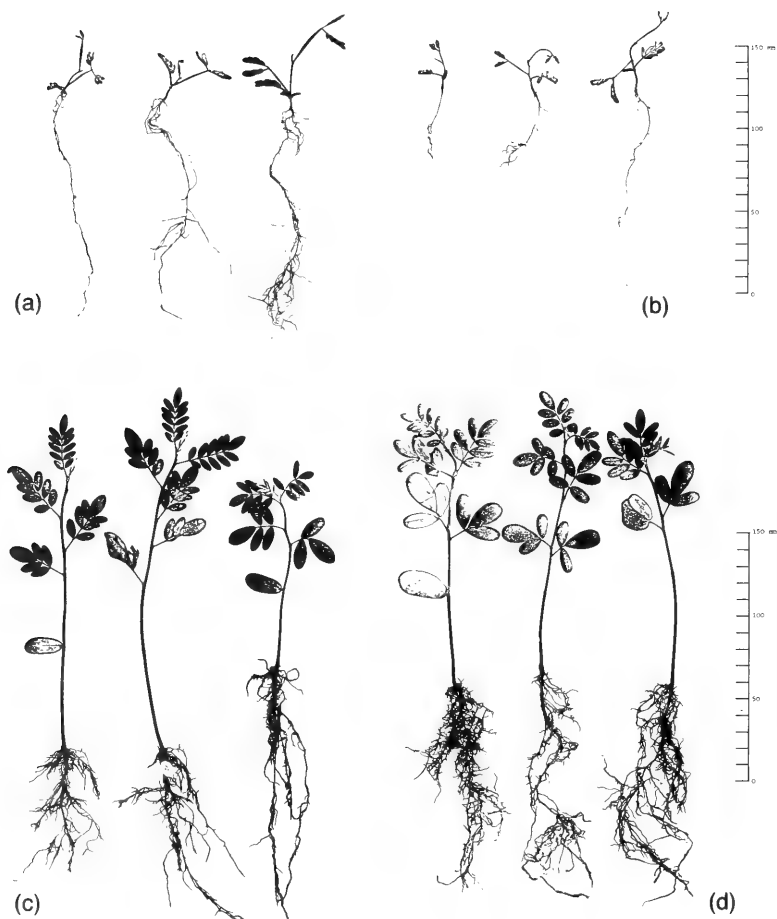


FIG. 5b.

Seedlings selected at random from pure and mixed stands of *Acacia*, *Virgilia*—showing effects of interaction.

- (a) 'Pure' *Acacia*
- (b) 'Mixed' *Acacia*—reduced root development and etiolated stems and leaves
- (c) 'Pure' *Virgilia*
- (d) 'Mixed' *Virgilia*—enhanced root development

TABLE 4a.
(ii) Tukey's Range Values = 0.05
[If confidence interval does not include 0—reject $H_0 = (S)$]

	Number of Weeks			
	2	4	6	9
Shoots	μ_{vi} vs. μ_{al} 0.84 → 3.36 (S)	0.02 → 3.76 (S)	0.30 → 3.70 (S)	0.44 → 3.76 (S)
	μ_{al} vs. μ_{ac} 0.31 → 2.83 (S)	0.51 → 4.29 (S)	1.27 → 4.67 (S)	2.02 → 5.34 (S)
	μ_{ac} vs. μ_{vi} 2.41 → 4.93 (S)	2.38 → 6.16 (S)	3.27 → 6.67 (S)	4.12 → 7.44 (S)
Roots	μ_{vi} vs. μ_{al} 2.37 → 10.43 (S)	11.52 → 45.08 (S)	-0.86 → 112.66 (NS)	-65.31 → 148.51 (NS)
	μ_{al} vs. μ_{ac} -2.63 → 5.43 (NS)	-12.38 → 21.18 (NS)	-35.06 → 78.46 (NS)	-32.31 → 181.51 (NS)
	μ_{ac} vs. μ_{vi} 3.77 → 11.83 (S)	15.90 → 49.48 (S)	20.84 → 134.46 (S)	9.29 → 223.11 (S)

μ_{vi} = Mean for *Virgilia*

μ_{al} = Mean for *Albizia*

μ_{ac} = Mean for *Acacia*

TABLE 4a.

Comparative rates of shoot and root growth in soil between all species: Anova F values and Tukey's ranges

(i) F observed values $F = 5.14$

	NUMBER OF WEEKS			
	2	4	6	9
Shoots	41.13	41.70	42.92	58.77
Roots	51.27	21.06	9.36	5.704

(Reject H_0 throughout)

TABLE 4b.

Comparative rates of shoot and root growth in soil between all species

(i) Dry mass in soil and interspecific comparisons

$F = 5.14$

Species	Total dry mass	Anova between species F_{OBS}	Tukey's confidence intervals [if not including 0 reject H_0 (S)]
<i>VIRGILIA</i>	.2790	43.6	VIRG. vs. ALB. 0.09 \rightarrow 0.26 (S) ALB. vs. ACAC. -0.01 \rightarrow 0.16 (NS) ACAC. vs. VIRG. 0.17 \rightarrow 0.34 (S)
<i>ALBIZIA</i>	.1018		
<i>ACACIA</i>	.0250		

(ii) Species Shoot/Root proportions (with standard deviations)

Species	$\frac{\text{Root length}}{\text{Shoot length}}$	$\frac{\text{Root weight}}{\text{Shoot weight}}$	$\frac{\text{Shoot weight}}{\text{Shoot length}}$	$\frac{\text{Root weight}}{\text{Root weight}}$
<i>VIRGILIA</i>	22.9 ± 6.2	2.71 ± 0.07	0.0118 ± 0.0010	0.00149 ± 0.00027
<i>ALBIZIA</i>	24.7 ± 3.3	0.873 ± 0.001	0.0132 ± 0.0009	0.00048 ± 0.00007
<i>ACACIA</i>	64.0 ± 21.2	0.68 ± 0.16	0.0305 ± 0.0124	0.00036 ± 0.00008

similar situation applies in the case of root growth in which *Albizia* ceases to show a significantly lower root length increment than *Virgilia* from week 6 onwards (Figure 6b, Table 4a).

Acacia differs from the other species with regard to relative shoot and root growth rates. The shoot length increment from week 2 to week 9 is virtually negligible, unlike the other species, whereas the root length increase is continuous, following a similar pattern to the others (Figures 6a and 6b).

The dry mass of the harvested plants showed no significance in difference between the means of *Albizia* and *Acacia* (Table 4b).

The proportions of root/shoot length increased in the following order: *Virgilia*, *Albizia*, followed by *Acacia* with the highest value (Table 4b). However, root/shoot dry-weight ratios showed the reverse trend.

Further inspection of the data in Table 4b shows that the shoot dry weight/shoot length values are in the approximate ratio of 15:17:38 for *Virgilia*, *Albizia*, *Acacia* respectively, indicating a significantly higher value for *Acacia*. However, the corresponding root dry weight/root length ratios, which are 15:5:4, show that *Virgilia* has the highest value for this parameter.

Thus it seems clear that both *Albizia* and *Acacia* produce greater lengths of root for less energy than *Virgilia*. Of less importance is the fact that *Virgilia* and *Albizia* allocate lower energy per length of stem than *Acacia*.

Finally some other general observations can be mentioned. *Albizia* shed its reddish-yellow embryonic seed cotyledons within the first three weeks after planting. The cotyledons of *Virgilia* and *Acacia*, on the other hand, turned green, hence photosynthetic, soon after germination and were retained for the full test period (Figure 6c). It was also noted that the *Acacia* seedlings did not develop phyllodes (characteristic of mature plants of this species) during the same period (Figure 6c). (In additional unharvested specimens these became apparent only at about 3 months of age).

COMPARATIVE ROOT AND SHOOT RATES FOR EACH SPECIES IN VERMICULITE WITH AND WITHOUT NUTRIENTS

The same experimental design and timing as described in the previous section were used for measuring root and shoot growth rates in this experiment. Instead of soil a Grade 3, coarse-grained vermiculite was used as a growth medium. Three replicate seedlings of each species and for each treatment were grown in two sets of nine root chambers.

To the first set of root chambers an application of 100 ml balanced nutrient solution was added to each seedling on a fortnightly basis for the full experimental nine week growth period. Concentrations of the nutrients added were as follows: $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O} = 1.35 \text{ g/l}$, $\text{NaNO}_3 = 0.6737 \text{ g/l}$, $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O} = 0.4188 \text{ g/l}$, $\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O} = 0.4727 \text{ g/l}$, $\text{K}_2\text{SO}_4 = 0.7500 \text{ g/l}$,

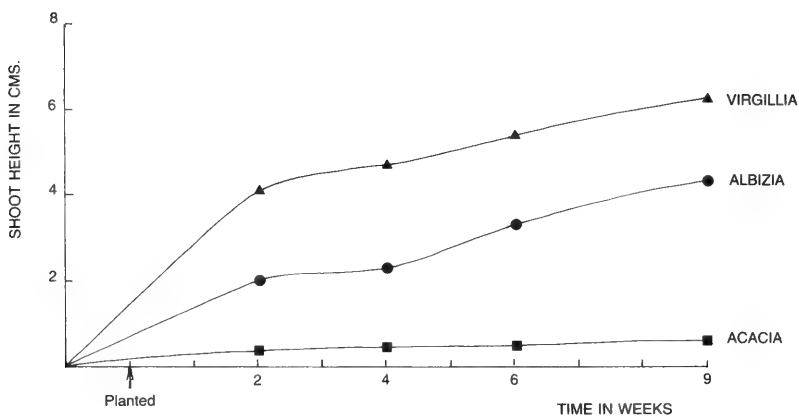


FIG. 6a.
Growth of shoots in root chambers.

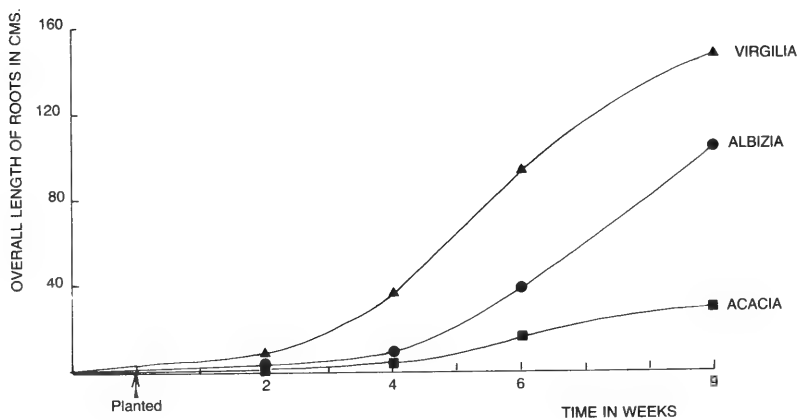


FIG. 6b.
Growth of roots in root chambers.

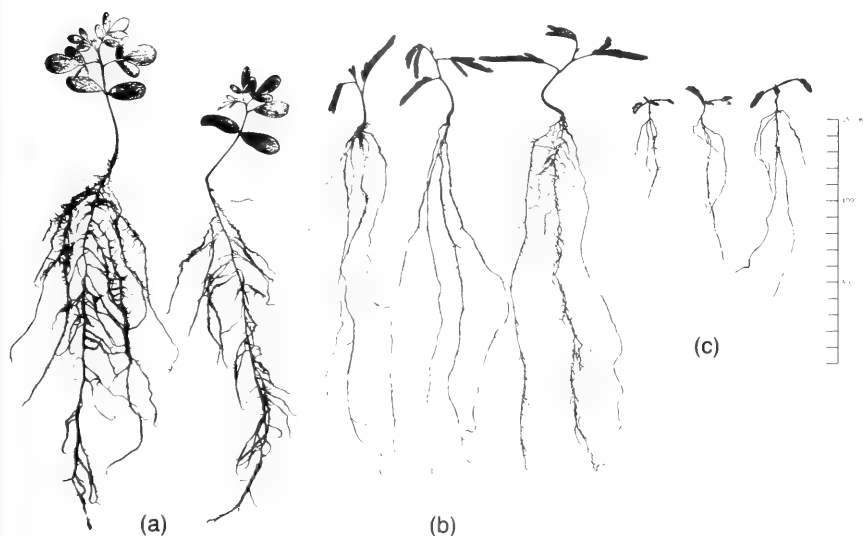


FIG. 6c.

Seedlings grown for nine weeks in root chambers in soil.

(a) *Virgilia*(b) *Albizia*(c) *Acacia*

Mg SO₄. 7H₂O = 0,5500 g/l, Ca Cl₂. 2H₂O = 0,285 g/l, FeNaEDTA = 0,0300 g/l, H₃ BO₃ = 0,858 × 10⁻³g/l, Mn Cl₂. 4H₂O = 0,543 × 10⁻³g/l, Zn SO₄. 7H₂O = 0,066 × 10⁻³g/l, Cu SO₄. 5H₂O = 0,024 × 10⁻³g/l, H₂Mo O₄. H₂O = 0,006 × 10⁻³g/l.

To the second seedling set no nutrients were added.

Results and discussion

Growth increments of shoots and roots were compared at each time interval for nutrient and non-nutrient treatments. In addition final dry weights for the seedlings were compared in the two treatments. Standard *t* tests were used to test significance throughout.

With the exception of root growth in *Albizia*, there were no significant differences between rates, or overall, shoot and root growths of any of the test species grown with or without the added nutrient solution (Table 5a, Figures 7a, b, c). With *Albizia* root growth was significantly reduced from week 6 to week 9 in the nutrient-treated plants, relative to the non-nutrient treated standards (Table 5a, Figure 7b).

Although the *Albizia* standards also showed a greater mean dry-weight than the nutrient-treated plants (Table 5b), this was not found to be significant (it may, however, imply a preference for very low nutrient levels). Similarly, no significance was found between mean dry weights for the separate treatments in *Virgilia* and *Acacia*, both of which showed lower *t* values than *Albizia* (Table 5b).

TABLE 5a.

Comparative rates of shoot growth in vermiculite, with and without added nutrients for each species: *t* values

Species		Number of weeks			
		2	4	6	9
VIRGILIA	Shoots	0.543 (NS)	0.660 (NS)	0.369 (NS)	0.168 (NS)
	Roots	0.095 (NS)	.045 (NS)	0.028 (NS)	0.082 (NS)
ALBIZIA	Shoots	0.823 (NS)	0.420 (NS)	0.530 (NS)	1.810 (NS)
	Roots	2.180 (NS)	2.400 (NS)	3.37 (S)	3.56 (S)
ACACIA	Shoots	1.797 (NS)	0.94 (NS)	1.200 (NS)	0.580 (NS)
	Roots	0.503 (NS)	2.160 (NS)	1.48 (NS)	0.58 (NS)

TABLE 5b.

Dry mass for each species with and without nutrients (*t* values compare effects of added nutrients)

Species	Treatment	Mean dry mass 9	<i>t</i> -Values
VIRGILIA	With nutrients	0.1952	0.395
	Without nutrients	0.1841	
ALBIZIA	With nutrients	0.1052	1.119
	Without nutrients	0.1372	
ACACIA	With nutrients	0.0176	0.626
	Without nutrients	0.0145	

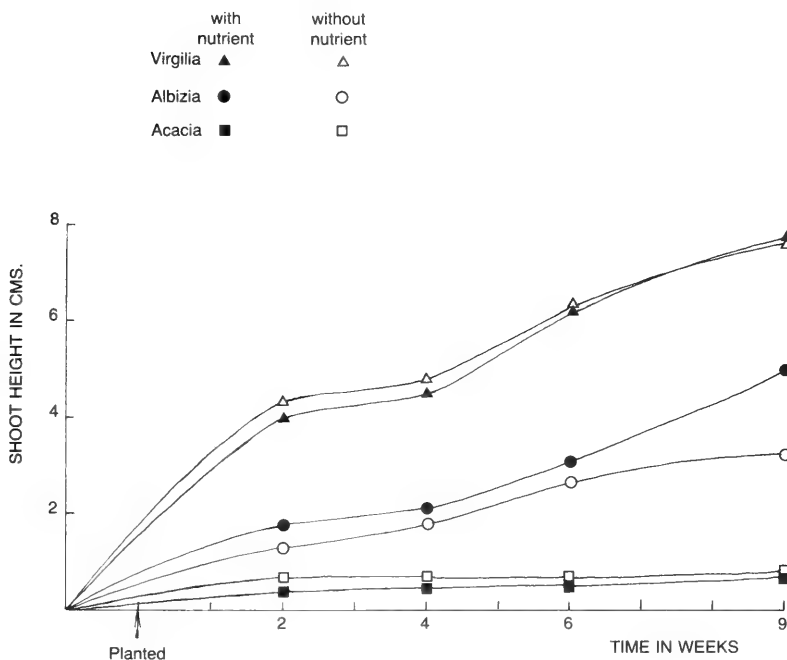


FIG. 7a.

Growth of shoots in nutrient and non-nutrient treated vermiculite in root chambers.

SOME MISCELLANEOUS OBSERVATIONS ON NATURAL SEED AND SEEDLING PREDATION AS WELL AS ON OVERALL SEED PRODUCTIVITY

In order to estimate whether differential seed predation may be a factor in reducing regeneration rates of any one of the test species, random samples of 50 seed pods were examined from trees of each species and the percentage of predated seeds was determined. In addition percentages of undeveloped, infertile seeds as well as the average numbers of seeds per pod for each species were measured.

Daily observations were also made on several seedlings of each species grown in the open during late autumn, to establish which species appeared most susceptible to seedling predation.

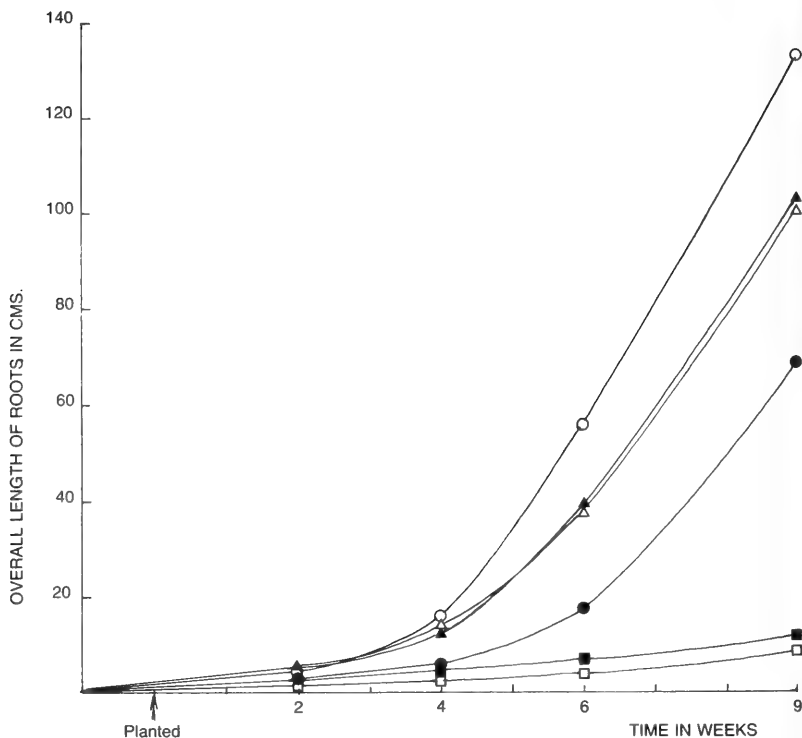


FIG. 7b.

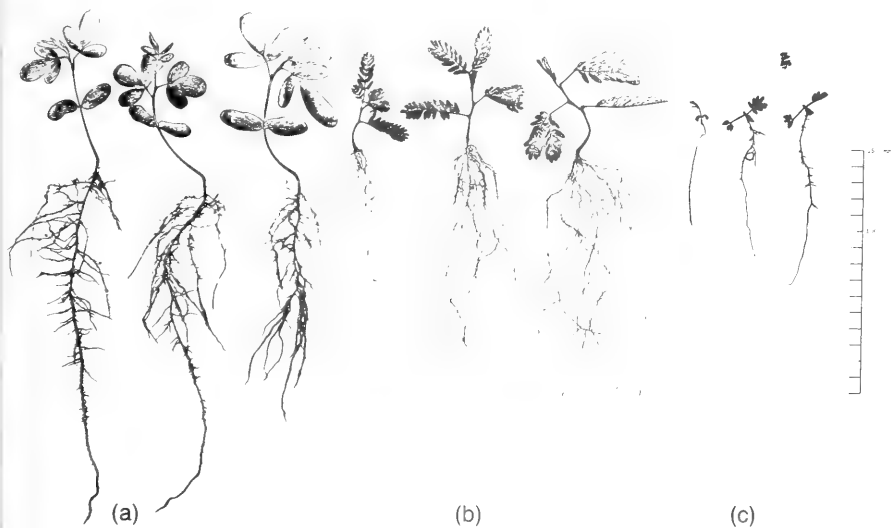
Growth of roots in nutrient and non-nutrient treated vermiculite in root chambers.

Results

The average numbers of seed per pod and the percentages of seed found to be infertile are presented in Table 6. With single samples and fairly similar values between the species, it is difficult to draw definite conclusions from these two sets of data. However, it does seem valid to conclude that predation is higher in the seed of *Virgilia* than that of *Albizia* and *Acacia*: 9.68 % predated in *Virgilia* compared with 0 % in both *Albizia* and *Acacia* (Table 6). Moth larvae (undetermined species) are considered to be the chief *Virgilia* seed predators in the sample studied.



(i) Nutrient treated vermiculite



(ii) Non-nutrient treated vermiculite

FIG. 7c.

Seedlings grown for nine weeks in root chambers with nutrient and non-nutrient treated vermiculite.

(a) *Virgilia*

(b) *Albizia*

(c) *Acacia*

TABLE 6.

Numbers of seed per pod, and percentages of infertile and predated seed for random samples of fifty seed pods taken from single trees for each species.

Species	Average number of seeds per pod	Percentage of infertile seed	Percentage of seed predated
<i>VIRGILIA</i>	3.72	5.91	9.68
<i>ALBIZIA</i>	9.90	3.03	0.0
<i>ACACIA</i>	7.38	6.78	0.0

The daily observation of seedlings grown outside, unprotected from predators, revealed heavy nocturnal leaf-feeding activities by crickets on the *Virgilia* seedlings—in most cases leading to mortality within about a month of germination. In contrast, seedlings of *Albizia* and *Acacia* remained unaffected by the crickets, and also apparently, by any other forms of visible predation. The same cricket has been observed during the late autumn in the field beneath *Virgilia* leaf litter (at Constantia Nek).

GENERAL DISCUSSION

Chipping of seed at the micropylar ends produced an extremely rapid germination in all the species. The results are comparable with those produced by the most effective seed germination enhancing treatments obtained by Clemens *et al.* (1977) during germination tests on five Australian acacias (including *Acacia longifolia*).

The various germination inhibitions recorded with increasing sensitivity in the order: *Virgilia*, *Albizia*, *Acacia*, are difficult to explain either on a theoretical or functional basis. Theoretically, some form of allelopathic interaction, similar to that described for *Acacia cyclops* and *Acacia saligna* (= *A. cyanophylla*) by Jones *et al.* (1963), might be operative. However, much recent criticism of earlier attempts to prove the presence of allelotoxins experimentally (Harper, 1977) precludes any direct conclusions about the exact nature of the inhibitions recorded. Oily exudates with strong aromatic odour, similar to those recorded for *Casuarina littoralis* litter in the inhibition of *Eucalyptus ovata* germination (Withers, 1977), were also noticed in the moistened macerated litters of all three test species. It is possible that some indirect inhibiting effect, such as lowered oxygen availability produced as a result of litter decay may have been operating rather than an allelochemic reaction.

It does seem feasible that leaf litter and seed-mix inhibitions (whatever their exact cause) could operate in the field. The existence of auto-inhibition, or mortality of germinating seeds due to decaying litter beds, beneath dense stands of *Acacia* and *Albizia*, is supported by the observation that seed regeneration is absent in these situations. However, it is more likely that this suggested type of inhibition is subsidiary to that of the enforced dormancy produced by impermeable seed coats, although the dormancy could become broken down by seed-coat decay. The tests also revealed that *Acacia* and *Albizia* seed are inhibited by the litters of one another as well as by that of *Virgilia*. This lack of specificity of action may well imply that many other types of litter could be inhibitory. Trials with non-leguminous indigenous *Kiggelaria africana* litter appear to support this theory (McDowell, pers. obs.). It is of interest to note that, among its other beneficial effects such as the breaking of the primary enforced seed-coat dormancy, fire may act to remove any inhibitory organic material from around the seed-store and thus enhance germination (Roux and Middlemiss, 1963; McPherson and Muller, 1969). It is reasonable to suppose that interspecific seed-litter inhibitions could act in the field and, therefore, artificially planted *Virgilia* might, by means of its accompanying leaf litter, act to curb the regeneration of *Acacia* and *Albizia*.

The number of long-lived seed-stores of pest Australian legumes is the most difficult problem pertaining to their control. For instance, in combination with other control measures the planting of *Eragrostis curvula* by the Grahamstown municipality in adjacent regions cleared of *Acacia longifolia* has so far successfully inhibited seed-store regeneration (McDowell, pers. obs.). *Eragrostis curvula* seed was the only species found to be immune to inhibition by cold-water extracts of the closely-related *Acacia cyclops* and *A. saligna* (Jones *et al.*, 1963).

Early seedling growth or vigour has been correlated with seed mass or energy (Salisbury, 1942; Grose and Zimmer, 1958) and thus may have some connection with the initial competitive vigour of the test species. However, *Albizia*, although possessing the greatest seed energy content, lagged behind *Virgilia* both in overall shoot length, root length and biomass increments as well as in competitive success. It could be argued that this results from the early shedding of the apparently non-photosynthetic cotyledons of *Albizia*, whereas the other two species retain their cotyledons as photosynthetic organs throughout. However, *Albizia* appears to have sufficient energy to overtake *Acacia* which possesses a far lower quantity of seed energy than either *Albizia* or *Virgilia*.

Newman (1973) maintains that shoot competition for light is the one obvious factor which can produce a competitive advantage of one species over the other. Results from the replacement series competition experiment tend to support this hypothesis, the increase of competitive inhibition for the three species corresponds with the increase in stem height. This correlation was also found in similar competition experiments involving seedlings of six *Eucalyptus* spp. (Burdon and

Pryor, 1975). Although this inference is valid, it cannot be fully verified unless the roots are isolated from one another during competition (Harper, 1977).

It is important to emphasize that, although the competitive enhancement/inhibition effects were largely significant at the stage of harvesting, the trends do not necessarily represent the final outcome, because the percentage mortality was negligible (never exceeding 15 % for any of the species in any culture). Possible reasons why the present situation does not reflect the final outcome may involve certain characteristics of the autecologies of *Albizia* and *Acacia*. For example, both species can evidently produce greater lengths of root with less energy than *Virgilia*, permitting an increase of nutrient transfer into the shoots, which is vitally important for light competition. In *Albizia* this is reflected by a later-developing, slightly faster growth rate for both shoots and roots. With *Acacia* the initial seed energy shortfall is slightly offset by the retention of photosynthetic seed cotyledons for up to 4 months (Milton, 1980), and also by the fact that no phyllodes had developed during the course of the experiment. If the experiment had been run for a longer period it is possible that the more robust phyllodes would have enhanced the photosynthetic capacity of *Acacia*, thereby increasing the production of its relatively low-energy roots, and hence shifting the competitive advantage to its favour.

However, it could be speculated that if the application of water in the experiment had not been optimal, mortality in the mixed stands relative to the pure might have been higher in the competitively inhibited plants, as the effect of species dominance appears to be most significant in the root biomass. If the latter were reduced in favour of an increase of energy to the shoots, in order to obtain access to the restricted light space, it is possible that the inhibited species might, by comparison with pure stand members, have become more susceptible to drought. In other words, too great a rate of transpiration might occur, relative to the capacity of water-uptake.

Among other environmental factors in the field which could alter the competitive balance between the species are differing moisture and nutrient availabilities of different soils (for example, *Virgilia* could represent a more vigorous competitor when growing at optimal conditions in a rich clay-loam similar to the experimental soil), in which the moisture content ranges from 35 to 50 % of dry mass (Phillips, 1926). However, *Albizia* may develop a competitive advantage over *Virgilia* in a poor, leached soil, as evidenced by its slightly improved performance in the non-nutrient vermiculite. An analogous situation may also apply in more advanced competition stages in which *Albizia* might tolerate lower nutrient levels. If this speculation is correct the addition of low fertilizer concentrations may boost the competitive power of *Virgilia* over that of *Albizia*. Only further experimentation can answer this question.

If one concedes that *Virgilia* occupies a similar niche to that of *Albizia* and *Acacia* what then is the prime reason for the greater geographical distribution of

the two alien species (most obvious in the Cape Peninsula)? This could be due to extensive plantings in the past (Shaunessy, 1980). Present knowledge of the behaviour of invading species also indicates that it is in the phases of germination and seedling establishment that success or failure in extending distribution is most critically determined (Harper, 1969). Superficial field examination of seed and seedling predation of the alien *Albizia/Acacia* relative to *Virgilia* reveals that at least part of the answer for *Virgilia*'s comparative lack of establishment may lie in its greater susceptibility to predation. Phillips (1926) records several agents, in addition to those described, which are destructive to both regenerative and adult stages of *Virgilia*.

If some biological means for curbing the regeneration of *Albizia* and *Acacia* similar to the insect control attempted for *Hakea* spp. (Neser, 1974, 1976) is introduced, it seems reasonable to suggest that interspecific competition by *Virgilia* might, if managed correctly, act as a subsidiary measure for the reclamation of regions infested by *Albizia* and *Acacia*. *Virgilia* has the additional advantage that it acts as a nurse plant to permit the seral establishment of other indigenous trees (Phillips, 1926), which may also play a rôle in the further suppression of *Albizia* and *Acacia*.

CONCLUSIONS

The observation of Harper (1977) that the most appropriate manner in which to detect differences in the ecologies of separate populations (or species) is to grow them together in mixtures has been, directly or indirectly, confirmed in this study. The broad hypothesis that the test legumes occupy similar niches has been verified and in addition several important, although minor, ecological differences have been highlighted by the comparative approach which was adopted in the experimental procedure.

It has been demonstrated that experiments using small samples can yield workable results. These results, analysed selectively, have provided some insight into what is broadly speaking an attempt to channel research directly into solving a pressing and urgent problem—that of controlling or curbing pest-plant encroachment by creating a natural replacement by desirable species (Piemeisel and Carsner, 1951). Thus it is hoped that this article has opened an alternative avenue of approach to the subject of pest-plant control, i.e. the careful manipulation of our own biological resources.

Future research should also involve field trials, along the lines being followed at present by Professor H. B. Rycroft, who is planting experimental plots of *Virgilia* on the *Acacia*-infested mountain slopes at Banhoek Valley, Cape Province. It also may prove of value to investigate other indigenous species that could play a similar out-competing rôle.

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 10-21

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10. *HAWORTHIA ANGUSTIFOLIA* Haw.

CHROMOSOME NUMBER: $2n = 14$ (Figs 1a, 1b).

ORIGIN OF MATERIAL: Hills E. of Grahamstown, C. G. Vosa 2074, living specimens at the Botany School, Oxford.

METHOD OF PREPARATION: Root-tip material, colchicine pretreatment, Feulgen (Acetic-orcein) staining.

OBSERVATIONS: This species and the eleven others in this contribution, have been collected in the wild by the authors and are preserved both as living specimens and as Herbarium material which is mostly kept at the National Botanic Gardens Herbarium at Kirstenbosch.

In all species the karyotype is strictly bimodal with eight large (L) chromosomes and six small (S) chromosomes.* Generally the short arm of at least three of the L-chromosomes and the long arm of all the S-chromosomes possess secondary constrictions of various width or terminally located reduced-staining segments. These secondary constriction gaps and these segments are allocyclic but generally do not form chromocentres in the interphase nuclei. Thus, they are not strictly heterochromatic in the accepted sense of the word but possess some of the attributes of heterochromatin and may prove to have great significance in the structure of the karyotype.

The nucleolar attachment is usually terminally located in the long arm of the L-chromosomes. It presents itself as a small satellite and is found mostly in a heterozygous condition in one or two or rarely three pairs of chromosomes. In the photographic illustrations the haploid karyotypes have been prepared with measurements taken by camera lucida on at least five metaphases in three or more clones.

*(see Brandham (1971) for discussion)

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1a

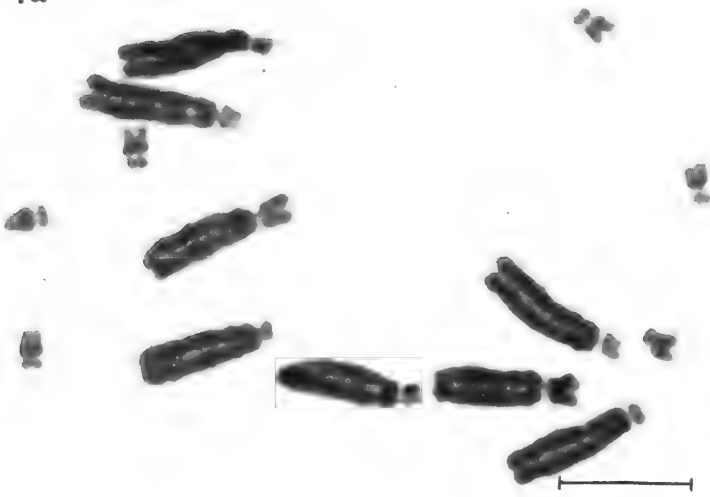
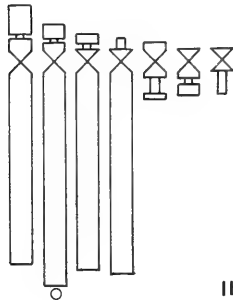


FIG. 1A
Mitotic metaphase in *H. angustifolia* Haw.



1b

FIG. 1B
Diagrammatic representation of the haploid karyotype of *H. angustifolia* Haw.

11. *HAWORTHIA ARACHNOIDEA* (L.) DuvalCHROMOSOME NUMBER: $2n = 14$ (Figs 2a, b).ORIGIN OF MATERIAL: Bavians, W. Laingsburg, *M. B. Bayer 2105* (NBG); *C. G. Vosa 2269*.

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: In this species the S1-chromosomes possess a rather long "euchromatic" segment in their long arm. These chromosomes could be used as a convenient marker (Fig. 2a, arrows).

2a

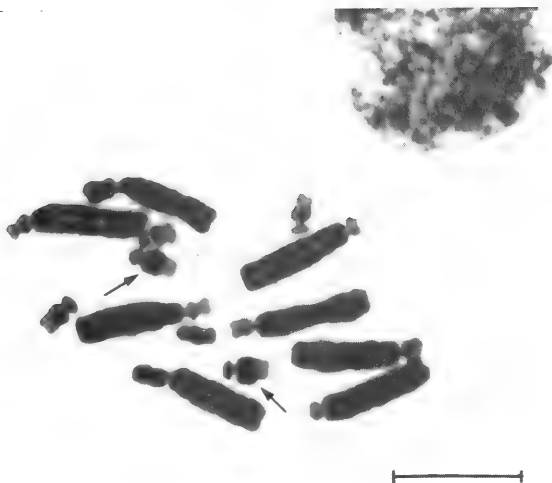
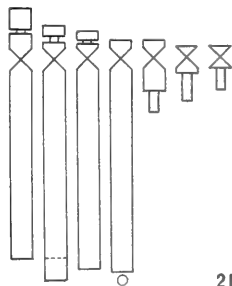


FIG. 2A

Mitotic metaphase in *H. arachnoidea* (L.) Duval. The arrows indicate the two S1-chromosomes with a long "euchromatic" segment in the long arm.



2b

FIG. 2B

Diagrammatic representation of the haploid karyotype of *H. arachnoidea* (L.) Duval.

12. *HAWORTHIA BAYLISSII* Scott

CHROMOSOME NUMBER: $2n = 14$ (Figs 3a, b).

ORIGIN OF MATERIAL: Oude Kraal, S. Somerset East, *M. B. Bayer 2052*; *C. G. Vosa 2235*.

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: Although morphologically very similar to *H. angustifolia* Harv. the chromosomes of this species show some differences particularly in the size of the allocyclic segments in L2 and L3-chromosomes and in all S-chromosomes.

This collection from the type locality does not correspond with the description for *H. baylissi* and it is supposed that the species was based on an aberrant plant. This is supported by co-types collected by L. D. A. Bayliss in the original collection and grown at Kirstenbosch, which also resembled *H. angustifolia* in most respects. Chromosomal differences observed here are therefore surprising.

3a

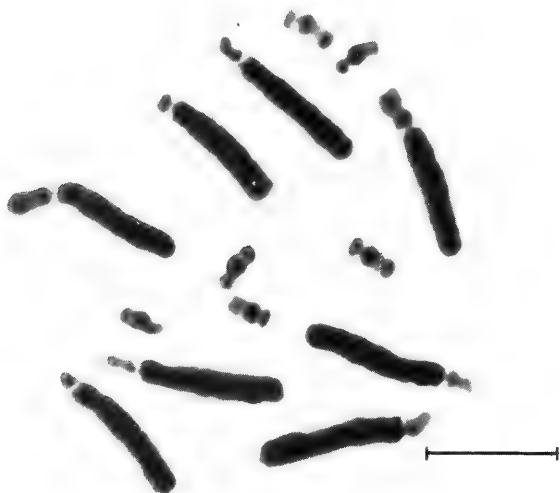
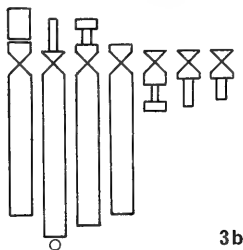


FIG. 3A
Mitotic metaphase in *H. baylissii* Scott.



3b

FIG. 3B
Diagrammatic representation of the haploid karyotype of *H. baylissii* Scott.

13. HAWORTHIA BLACKBURNIAE Barker

CHROMOSOME NUMBER: $2n = 14$ (Figs 4a, b).

ORIGIN OF THE MATERIAL: Ladismith, C. G. Vosa 2035.

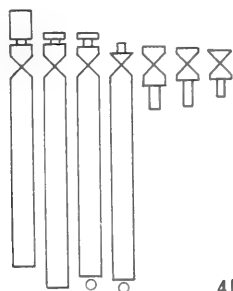
METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The S-chromosomes possess relatively long, distally located allocyclic segments.

4a



Mitotic metaphase in *H. blackburniae* Barker. Note the long allocyclic segments in the long arms of the S-chromosomes.



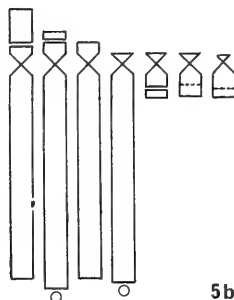
4b

FIG. 4b

Diagrammatic representation of the haploid karyotype of *H. blackburniae* Barker.

14. **HAWORTHIA BOLUSII** Bak.CHROMOSOME NUMBER: $2n = 14$ (Figs 5a, b).ORIGIN OF MATERIAL: Graaff Reinet, *M. B. Bayer* 2022; *C. G. Vosa* 2230.

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: Some details of chromosome morphology are very interesting, especially in relation to the S-chromosomes which provide a good marker for separating this species from *H. arachnoidea* (L.) Duval.FIG. 5A
Mitotic metaphase in *H. bolusii* Bak.FIG. 5B
Diagrammatic representation of the haploid karyotype of *H. bolusii* Bak.

15. *HAWORTHIA COOPERII* Bak.CHROMOSOME NUMBER: $2n = 14$ (Figs 6a, b).

ORIGIN OF MATERIAL: Keiskammahoek, C. G. Vosa 2271.

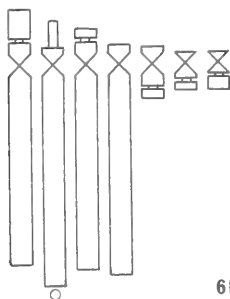
METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The chromosome morphology of this species resembles that of *H. nortieri* Smith (q.v.), but the S-chromosomes have a distally located non-allocyclic segment.

6a



FIG. 6A

Mitotic metaphase in *H. cooperii* Bak.

6b

FIG. 6B

Diagrammatic representation of the haploid karyotype of *H. cooperii* Bak.

16. *HAWORTHIA HERBACEA* (Mill.) StearnCHROMOSOME NUMBER: $2n = 14$ (Figs 7a, b).

ORIGIN OF MATERIAL: Hammonshof Pass, C. G. Vosa 1974.

METHOD OF PREPARATION: As in 10.

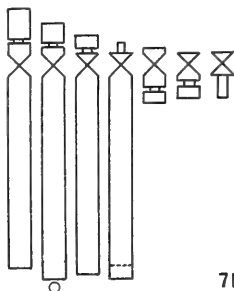
OBSERVATIONS: The overall chromosome morphology of this species is within the normal variation found in the genus, however, the L4-chromosome has a very distinct constriction in the distal part of the long arm (Fig. 7a, arrows).

7a



FIG. 7A

Mitotic metaphase in *H. herbacea* (Mill.) Stearn. Note the secondary constriction in the distal part of the long arm of the L4-chromosomes (arrows).



7b

FIG. 7B

Diagrammatic representation of the haploid karyotype of *H. herbacea* (Mill.) Stearn

17. *HAWORTHIA NORTIERI* var. *NORTIERI* SmithCHROMOSOME NUMBER: $2n = 14$ (Figs 8a, b).

ORIGIN OF MATERIAL: Matsikamma Mts., Vanrhynsdorp, M. B. Bayer 1972; C. G. Vosa 2236.

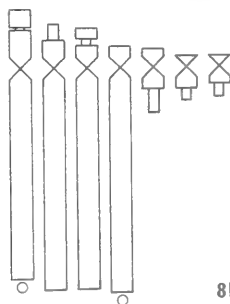
METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The overall chromosome morphology is very similar to *H. semi-viva* (v.Poelln.) Bayer (q.v.), but the L1-chromosome has only one secondary constriction in its short arm.

8a



FIG. 8A

Mitotic metaphase in *H. nortieri* var. *nortieri* Smith.

8b

FIG. 8B

Diagrammatic representation of the haploid karyotype of *H. nortieri* var. *nortieri* Smith.

18. *HAWORTHIA SEMIVIVA* (v. Poelln.) BayerCHROMOSOME NUMBER: $2n = 14$ (Figs 9a, b).ORIGIN OF MATERIAL: Williston, *M. B. Bayer 1274*; *C. G. Vosa 2258*.

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The short arm of the L1-chromosome has two distinct secondary constrictions (Fig. 9a, arrows).

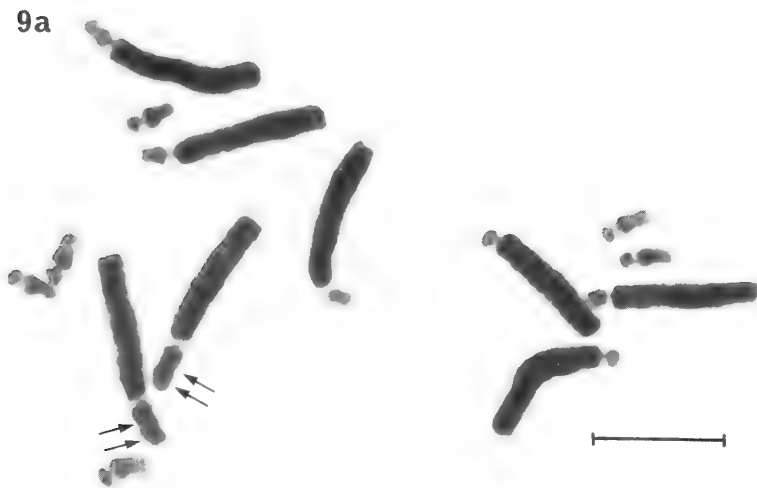
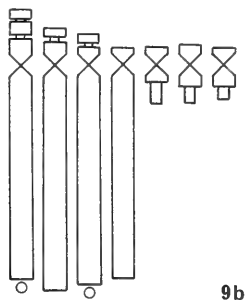


FIG. 9A

Mitotic metaphase in *H. semiviva* (v. Poelln.) Bayer. Note the two secondary constrictions in the short arm of the L1-chromosomes (arrows).



9b

FIG. 9B

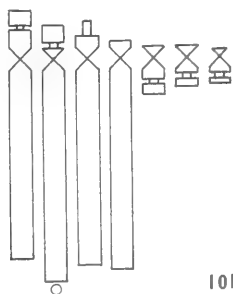
Diagrammatic representation of the haploid karyotype of *H. semiviva* (v. Poelln.) Bayer.

19. **HAWORTHIA TRANSLUCENS** Haw.CHROMOSOME NUMBER: $2n = 14$ (Figs 10a, b).ORIGIN OF MATERIAL: Hellspoort (Grahamstown), *C. G. Vosa* 2136.

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: Chromosome morphology very similar to *H. cooperii* Bak. (q.v.), but with a relatively shorter short arm in the L1-chromosome.

10a

FIG. 10A
Mitotic metaphase in *H. translucens* Haw.

10b

FIG. 10B
Diagrammatic representation of the haploid karyotype of *H. translucens* Haw.

20. *HAWORTHIA TRUNCATA* SchonlandCHROMOSOME NUMBER: $2n = 14$ (Figs 11a, b).ORIGIN OF MATERIAL: var. *tenuis*. De Rust, M. B. Bayer s.n.; C. G. Vosa 2252; var. *truncata*. Oudtshoorn, M. B. Bayer s.n.; C. G. Vosa 2251.

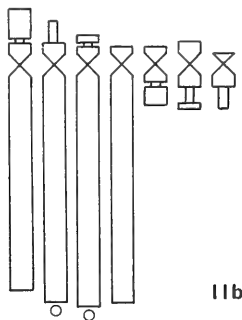
METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The illustrations refer to the var. *tenuis*. The two varieties of this species are indistinguishable chromosomally. In cultivation at the Karoo Botanic Garden, the variety *tenuis* has been observed to lose its characteristic small form and varietal status is dubious on that score too.

11a



FIG. 11A
Mitotic metaphase in *H. truncata* var. *tenuis* Schonland.



11b

FIG. 11B
Diagrammatic representation of the haploid karyotype of *H. truncata* var. *tenuis* Schonland.

21. **HAWORTHIA UNICOLOR** var. **VENTERI** (v.Poelln.) BayerCHROMOSOME NUMBER: $2n = 14$ (Figs 12a, b).ORIGIN OF MATERIAL: 4 km west of Vanwyksdorp, *M. B. Bayer s.n.* (KG 555/71)

METHOD OF PREPARATION: As in 10.

OBSERVATIONS: The chromosome morphology of this species is interesting. The usual secondary constriction is absent from the short arm of the L1-chromosome but a very prominent one is located in the distal part of its long arm (Fig. 12a, arrows).

12a

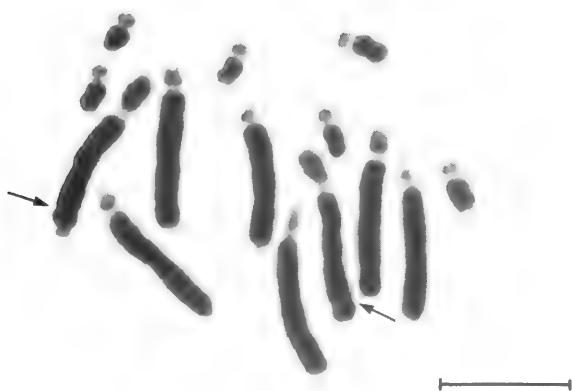
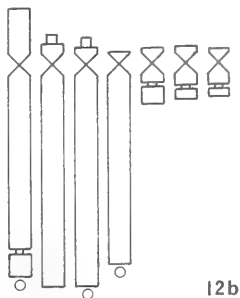


FIG. 12A

Mitotic metaphase in *H. unicolor* var. *venteri* (v. Poelln.) Bayer. Note the prominent secondary constrictions in the long arm of the L1-chromosomes (arrows) and the absence of the secondary constriction in the short arm of the same chromosomes.



12b

FIG. 12B

Diagrammatic representation of the haploid karyotype of *H. unicolor* var. *venteri* (v.Poelln.) Bayer.

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ABOVE-GROUND BIOMASS OF AUSTRALIAN ACACIAS IN THE SOUTHERN CAPE, SOUTH AFRICA

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ABSTRACT

Dimension analysis was used to estimate above-ground biomass of thickets of exotic Australian acacias, chiefly *Acacia cyclops* Cunn. ex G. Don. and *A. saligna* (Labill.) H. Wendl., at 15 sites in the southern Cape, South Africa. The thickets contained an average density of 5 200 acacia trees/ha; the trees varying between 5 and 10 m in height. A mean above-ground biomass of 104 t/ha (dry mass) was obtained, which is about three times the biomass of indigenous Fynbos vegetation. Acacia biomass composition on a dry mass basis was as follows: 64,7% wood, 22,8% brown twigs and 12,9% browse. Pods and seeds contributed 41,2% to the browse mass during November, but only 13% between February and July. The economic feasibility of utilising acacia biomass as a means of controlling these woody weeds is considered.

UITTREKSEL

BOGRONDSE BIOMASSA VAN AUSTRALIESE AKASIAS IN DIE SUID-KAAP, SUID-AFRIKA

Dimensionele ontleding is gebruik om die bogrondse biomassa van ruigtes uitheemse Australiese akasias, hoofsaaklik *Acacia cyclops* Cunn. ex G. Don. en *A. saligna* (Labill.) H. Wendl., by 15 persele in die Suid-Kaap, Suid-Afrika, te skat. Die ruigtes het 'n gemiddelde digtheid van 5 200 akasia bome/ha gehad; die bome tussen 5 en 10 m hoog. 'n Gemiddelde bogrondse biomassa van 104 t/ha (droë massa) was verkry, wat ongeveer driemaal die biomassa van inheemse Fynbos plantegroei is. Akasia biomassa samestelling op 'n droë massa basis is as volg: 64,7% hout, 22,8% bruin takkies en 12,9% takvoer. Peule en saad dra 41,2% by tot die takvoermassa gedurende November by, maar slegs 13% tussen Februarie en Julie. Die ekonomiese uitvoerbaarheid om akasia biomassa te gebruik as 'n metode om die houtagtige onkruid te beheer, word oorweeg.

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*This paper constitutes part of the commemoration of the 21st anniversary of the establishment of the Percy FitzPatrick Institute of African Ornithology.

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INTRODUCTION

Australian acacias, chiefly *Acacia cyclops* Cunn. ex G. Don. and *A. saligna* (Labill.) H. Wendl., are feral in the southern Cape Province, South Africa, where they have spread in thickets over some 3 000 km² (Taylor, 1975), reducing the farming and recreational value of land and ousting the indigenous vegetation (Hall, 1979). Mechanical or chemical clearing of the thickets for the establishment of pasture or crops is currently uneconomic in areas where the soil is inherently poor in plant nutrients. Consequently, much of the land occupied by the acacias remains unused, and they continue to spread and replace the indigenous vegetation. Direct use of the acacias for goat farming has failed, because the sale value of the animals does not meet the cost of food supplements and fencing (C. Uys and H. W. Sharp, pers. comm.). Thus, it is unlikely that significant reductions in the present extent and spread of the exotic acacias will occur in the foreseeable future, unless a commercial market for acacia products can be developed to help offset the cost of clearing operations.

There are indications that products of the Australian acacias have potential for commercial use. The photosynthetic tissue, pods, bark, twigs and stem-wood all have some putative value as animal fodder supplements, fuels (including alcohols, methane and charcoal), chemicals (including tannins and acetone) or fibres (Anon., 1978; Goodricke, 1978). However, before the economic feasibility of exploiting the usable products can be gauged, it is necessary to have information on the above-ground biomass of acacia thickets per unit area, and its distribution in the various components of the plant. Here we present regression equations relating mass of acacia products to stem diameter, and we consider the biomass yield, and its economic implications, of typical acacia thickets in the southern and western Cape.

STUDY AREAS AND METHODS

Destructive sampling to determine the relationship between basal diameter and the mass of the tree components was carried out at four localities between February and November, 1978. We sampled seven *A. saligna* and nine *A. cyclops* trees at the School for Boys near Faure (referred to as the Faure site), on the Cape Flats 20 km south east of Cape Town; five *A. saligna* trees near Cape Point in the Cape of Good Hope Nature Reserve 40 km south of Cape Town; 30 *A. longifolia* (Andr.) Willd. saplings in the grounds of the University of Cape Town on the lower slopes of Table Mountain; and, 372 *A. longifolia* and *A. saligna* seedlings in a burned thicket near Constantia Nek 15 km south west of the University.

Stand characteristics were recorded in 15 sample plots at eight localities in the southern Cape, which were infested with pure or mixed stands of *A. cyclops*, *A. saligna*, *A. longifolia* and *A. melanoxylon* R. Br. (Appendix 1A). Within

each study plot (variable area) each individual acacia was assigned to a stem diameter class (measured 100 mm above the ground), and the number of trees in each class was recorded. Percentage projected canopy cover, mean tree height, the approximate age of the stand (as reported by persons familiar with the area), percentage projected canopy cover of other genera, and soil texture, were also recorded.

Biomass was estimated by means of dimension analysis. This method, in which allometric relationships for trees of various sizes are applied to the size distribution in the stand, is considered to be best for estimating standing crop of woody stands older than 2–5 years (Madgwick, 1970; Whittaker & Marks, 1975). It has been applied successfully to temperate forest (Satoo, 1970; Whittaker & Woodwell, 1968), eucalypt forest (Attiwill, 1979), African savanna-woodland (Huntley, 1977) and *Acacia mearnsii* De Wild. plantations (Schönau, 1978).

Acacia cyclops and *A. saligna* trees with stem diameters ranging from 20–160 mm were measured for total height and canopy height and diameter, and then divided, after felling, into the following components: wood exceeding or equal to 20 mm diameter, green matter (including foliage, young shoots and immature pods), and mature pods. All components were weighed in the field, using 20 and 5 kg Pesola spring balances.

A dry mass : wet mass ratio was calculated from subsamples of each component, which were taken in polythene bags to the laboratory, weighed, dried to constant weight at 90 °C, and reweighed on a Mettler top pan balance. Estimates of numbers of pods per unit mass, and of bark mass : wood mass ratio, were also obtained from subsamples. The total biomass (or mass of a single component) per unit area of an acacia thicket was calculated, using Satoo's (1970) equation

$$W = (w'n)$$

where W is the total biomass (or mass of a particular component) per unit area; w' is the total (or component) mass of an average member of the size class; and, n is the number of trees per unit area in the approximate size size class. w' was obtained from the regression relationship between stem diameter of a tree and the mass of its components.

RESULTS

Biomass and stem diameter of trees

Acacia cyclops and *A. saligna* biomass was strongly correlated with stem diameter ($r \geq 0.93$ Figures 1 & 2, Appendix 2). This applied to both the dry and wet mass of the whole tree and of its component parts (wood, twigs and browse). The relationship between the common logarithms of diameter and mass was

linear, and the standard errors for predicted mass (y) values were small for both species. The value of double logarithm regression for predicting biomass from a stem dimension, which was pointed out by Madgwick (1970), Satoo (1970) and Whittaker & Marks (1975), is confirmed yet again by our results.

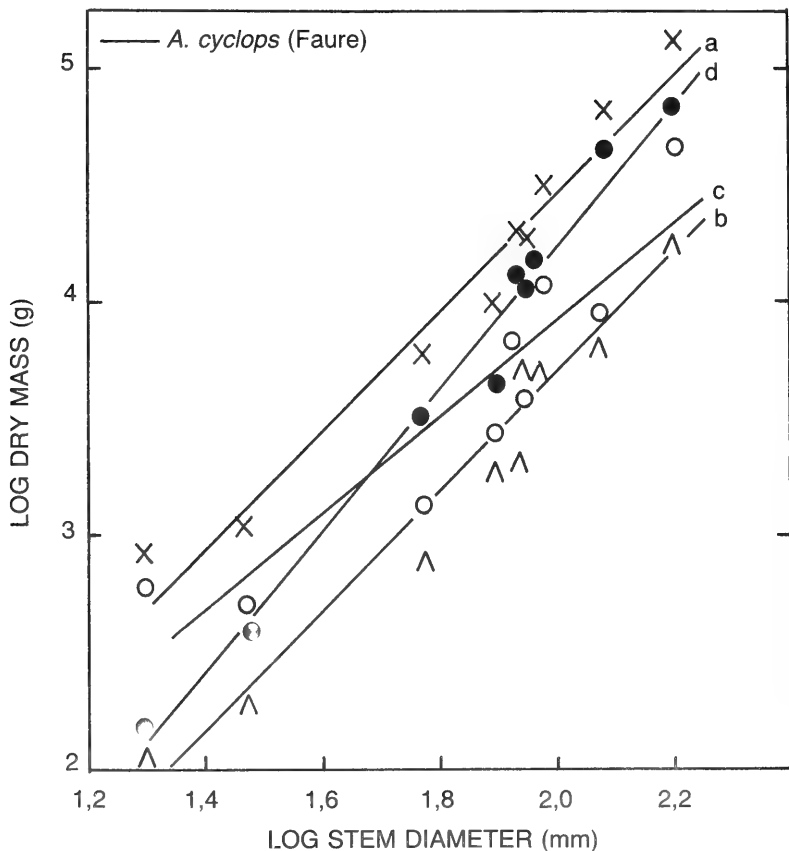


FIG. 1.

The relationship between log above-ground biomass (dry mass) and log stem diameter of *A. cyclops* trees at Faure. X = total above-ground mass of tree; ● = wood and bark; ○ = twigs; and △ = foliage (browse). For regression equations see Appendix 2.

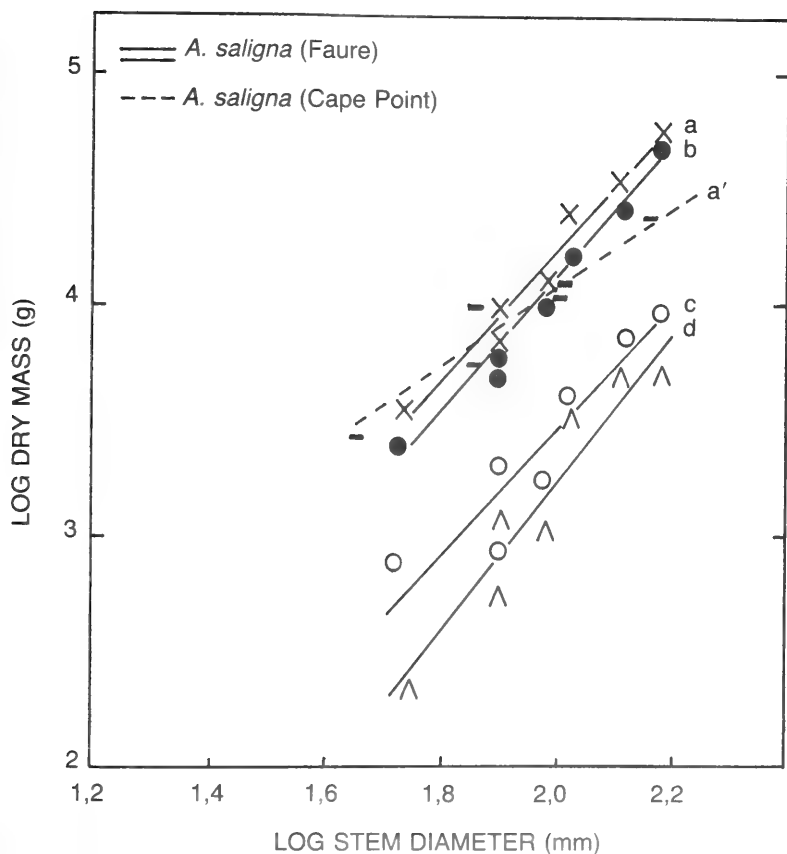


FIG. 2.

The relationship between log above-ground biomass (dry mass) and log stem diameter of *A. saligna* trees at Faure (continuous lines) and Cape Point (dashed line). X and — = total above-ground mass of tree; ● = wood and bark; ○ = twigs; and △ = foliage (browse). For regression equations see Appendix 2.

The slope of the regression of log. total dry mass on log. stem diameter of *A. saligna* at Cape Point differed from that based on the Faure sample ($t_{calc.} = 2.43$; $t_{(2),9} = 2.26$; $P = 0.05$; Figure 2). This difference can be attributed to the relatively exposed nature of the Cape Point site. Tree height there appeared to be limited by wind pruning, so that, for trees 4–5 m in height, stem

diameter increments were not reflected in height increments (Fig. 3), and the plants remained shrubby rather than tree-like in appearance. There was no significant difference between the regressions for *A. cyclops* and *A. saligna* at the Faure site. ($t_{calc.} = 0,07$; $t_{(2),12} = 2,18$; $P = 0,05$).

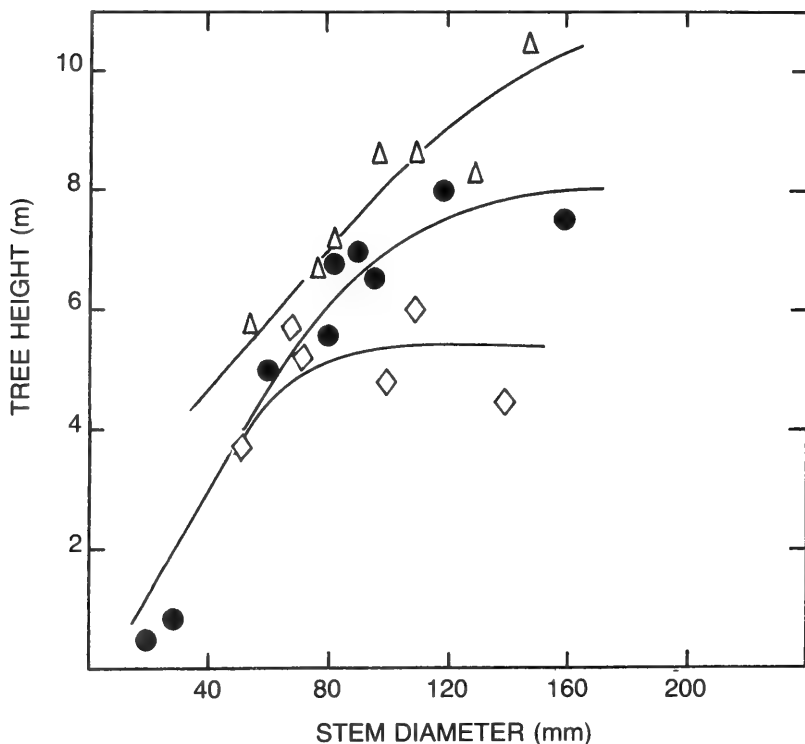


FIG. 3.

The relationship between tree height and stem diameter of *A. saligna* at Faure (Δ); *A. saligna* at Cape Point (◇); and, *A. cyclops* at Faure (●). Curves fitted by eye.

Biomass of stands and size-class distribution of trees

The product of the mass of a tree of average diameter and tree density per unit area was not used to estimate the biomass of a stand of trees, because the distribution of both tree abundance and mass in size classes was skewed strongly (Fig. 4). Moreover, acacia thickets are often associations of two or more species

differing in their stem diameter:mass relationship and in the allocation of biomass to stem and canopy. Consequently, it was necessary to sample the frequency distribution of the stem diameter size classes in a thicket. The values used in estimating the biomass contribution of each size class and species within a stand are derived from the regression equations (Appendix 2). The total stand biomass (B) per unit area was calculated from the equation

$$B = \sum_{i=1}^n f_i b_i$$

where f_i is the frequency in the i -th diameter class, b_i is the biomass for the mid diameter tree in class i , and $i = 1, n$.

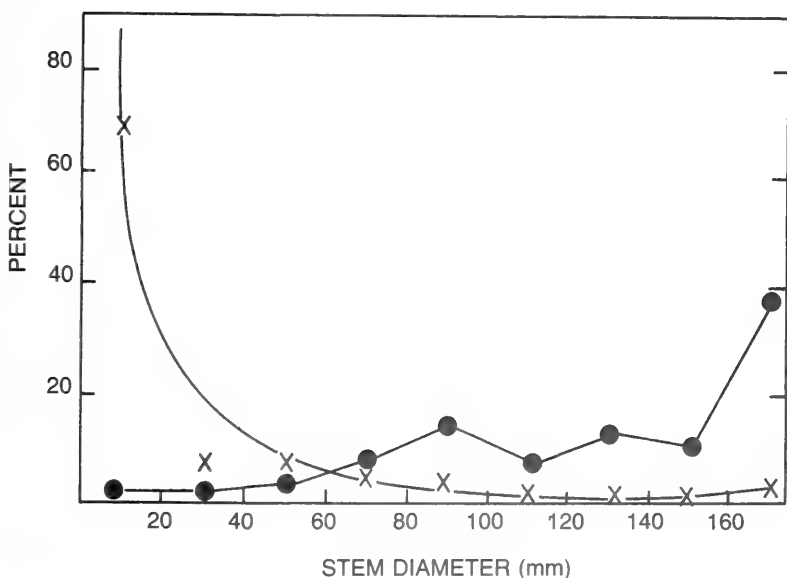


FIG. 4.

Percentage frequency of trees and percentage total biomass (dry mass) in mixed stands of *Acacia* spp. in the southern Cape, in relation to stem diameter classes. Line connecting crosses represents number of trees, and line connecting dots represents biomass. (Based on average of values in Appendix 1.)

In spite of the variation in habitat, age of trees, and species composition of the 13 mature acacia stands included in this study, the standard error of the average dry mass of a thicket (104 t/ha) was only 13 %. Stem diameters of trees in these stands ranged from <10 mm to >160 mm, and although only 2 % of all measured trees exceeded 160 mm in diameter, they should make the largest single contribution (38 %) to total stand biomass (Fig. 4), if the extrapolation of the regression line in Figure 1 is valid.

After clearing by fire, the acacias considered here regenerate in large numbers. Densities of up to 3×10^6 seedlings/ha were recorded nine months after a fire on the Cape Peninsula. The young plants grow rapidly. Populations thin quickly until, after five years, density is similar to that of mature stands (Fig. 5). However, numerous seedlings <10 mm in diameter and generally <100 mm in height may occur in mature stands, particularly during the rainy season. Field observations indicate that some seed germinates each year, but that seedlings have a low chance of surviving under a mature canopy. Hence, seedlings <10 mm in diameter were considered to be ephemeral, and are excluded from the values in Figure 5.

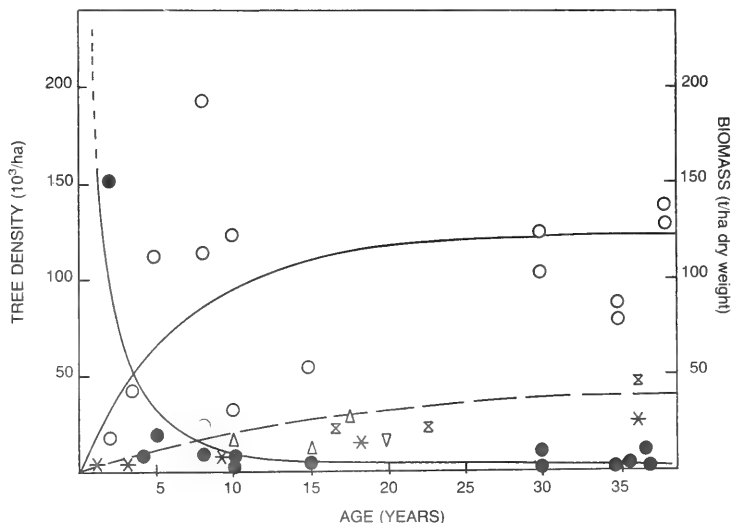


FIG. 5.

Density of trees and biomass (dry mass) in mixed stands of *Acacia* spp. in the southern Cape, and biomass (dry mass) of mediterranean-type vegetation, in relation to age. ● = density and ○ = biomass of acacia trees (based on averages of values in Appendix 1 and regression equations in Appendix 2). * = Australian Heath (Specht, 1969); x = French and Californian vegetation (Mooney, 1977); △ = Fynbos (Kruger, 1977) and ▽ = Fynbos (Kathan, 1979).

Biomass of the components of trees

All components of *A. cyclops* have a significantly ($P = 0.01$) higher dry mass per unit fresh mass than *A. saligna* (Table 1). The relatively low moisture content (34 %) of *A. cyclops* might be related to the species' natural occurrence in drier, windier habitats, and closer to marine shores, than *A. saligna*. The higher specific density of its wood explains why *A. cyclops* is more popular than *A. saligna* as a heating and cooking fuel.

TABLE 1

A comparison of mean dry:wet biomass ratios between *A. cyclops* ($n = 9$ trees) and *A. saligna* ($n = 7$ trees) in the south-western Cape. (Figures in parentheses are C.V.)

Component	<i>A. cyclops</i>	<i>A. saligna</i>	Significant difference
Wood (> 20 mm diam.)	0.685 (1.6)	0.610 (3.4)	**
Brown twigs	0.727 (4.1)	0.470 (2.3)	**
Foliage & green twigs	0.429 (2.6)	0.361 (4.4)	**
Pods	0.380 (—) ^a	0.320 (—) ^a	—
.....	0.906 (1.3) ^b		
Total for tree	0.660 (1.6)	0.534 (2.7)	**

^a Mature green pods

^b Non-deciduous ripe pods

** Significance level = 0.01

Used in conjunction with the dimension: mass regression equations (Appendix 2), stem diameter class frequencies (Appendix 1) and dry mass:wet mass ratios (Table 1), the values in Appendix 3 allow prediction of the amounts of wood, twigs, foliage and pods produced by stands of *A. cyclops* and *A. saligna*.

Clearly wood makes up the major portion of the total biomass (Fig. 6). The combined average biomass distribution of the two species is presented, since they were found to be equally common in the thickets sampled. However, where the two species grow under similar conditions, *A. cyclops* tends to be more highly branched, with the woody fraction (wood and bark) amounting to 57 % of the plant's total dry mass, as opposed to a comparable 72 % in *A. saligna*. The relatively large twig component of *A. cyclops* (Appendix 3) suggests that wood production per tree of a given diameter is lower than in *A. saligna*. This is not the case, however, because the relatively low wood volume is offset by the high wood density of *A. cyclops*.

Comparison between acacia and indigenous vegetation biomass

The above-ground, dry weight biomass of the exotic acacia thickets (104 t/ha) in the southern Cape is similar to that of forests (120 t/ha) in arid sub-tropical

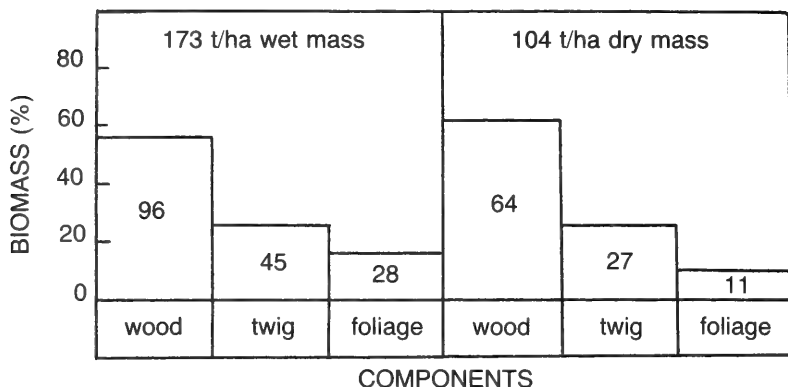


FIG. 6.

Distribution of biomass components in mixed stands of *Acacia* spp. in the southern Cape. (Based on values in Appendices 1 & 3.)

regions, whereas the biomass of the indigenous Cape Fynbos is typical of low shrub communities (20–30 t/ha) in these regions (Rodin *et al.*, 1975). Fynbos and similar mediterranean-type shrublands in France and Australia mature more slowly than the acacia thickets considered here and, when mature, the indigenous vegetation seldom attains a biomass greater than 40 t/ha (Fig. 5). Hence, after a fire, regenerating acacias rapidly outgrow Fynbos plants and maintain a position of dominance. The moisture content of *A. cyclops* (34 %) and *A. saligna* (47 %) is, however, similar to that of Fynbos (42–49 % Kathan, 1979; 32–44 % Kruger, *in litt.*) and Australian heath (30–42 % Specht, 1969).

Allocation of biomass in the acacias is similar to that of small trees in temperate regions (Whittaker & Woodwell, 1968; Satoo, 1970). In larger trees more of the biomass is allocated to wood than in shrubs, where more is allocated to twigs and foliage. The negative and exponential relationship between tree abundance and stem diameter found in the acacia thickets is similar to that existing in the indigenous forests of the southern Cape (Van Laar & Lewark, 1973).

DISCUSSION

The above-ground biomass of the exotic acacia thickets in the southern Cape is comparable to that estimated for two ten-year-old *A. mearnsii* plantations in Natal (110 and 148 t/ha Schönau, 1978). However, whereas wood >20 mm in diameter accounts for 57 % and 72 % of the dry mass of *A. cyclops* and *A. saligna* respectively, it makes up 77–80 % of *A. mearnsii* plantation trees; foliage contributing only 5 % to total plantation biomass (Schönau, *op. cit.*). Self-established thickets of exotic acacias have a mean density of 5 267

(CV = 21 %) trees/ha (Appendix 1B), whereas 1 280–1 440 trees/ha occur in *A. mearnsii* plantations. The wild thickets have a median basal diameter of 90 mm, and vary between 5 and 10 m in height, whereas ten-year-old *A. mearnsii* plantation trees have a breast height diameter of 125 mm and average 17.5 m in height (Schönau, *op. cit.*). These differences suggest that self-sown acacia thickets in the southern Cape produce less wood, and will be more difficult and expensive to harvest than plantation trees.

Although in Australia many acacia species are used as drought fodder, supplementary high-energy feeds and mineral licks are necessary (Everist, 1969). In Natal, leaves and twigs of *A. mearnsii* containing 5.7 % tannin were unpalatable to sheep. Moreover, since this fodder has low digestibility, the costs of its collection and processing are unwarranted in spite of its relatively high (18 %) protein content (Goodricke, 1978).

Harvesting and chipping of plantation biomass for use in the production of methane, alcohol, acetone or yeast, or simply for heating water to drive steam engines, is capital intensive. In order to produce methanol economically, for instance, it would be necessary to supply 1 million t/yr of plantation biomass, on a sustained yield basis, from an area within a 100 km radius of the processing plant (Anon., 1978). Clearly, felling, and the elimination of the non-uniform, self-sown acacia thickets in the southern Cape does not meet the prerequisites for the production of methane, alcohol or yeast on a commercial basis, and the necessity of hand gathering, would add to the production costs of acacia fodder.

CONCLUSION

At present there appears to be little possibility of financing the clearing of acacia thickets in the southern and western Cape, on a large scale, with revenue from the sale of the products. However, brush chippers are already being used by some South African municipalities for the demolition of thickets, and research into the best way of using the chips without further dispersing acacia seeds is needed. It also seems worthwhile to investigate the potential utility of acacia chips in small-scale methane digesters, charcoal burners and composters for small-holdings, and the effects of processing methods on the palatability and food value of acacia forage. The high productivity of the exotic acacias on soils generally considered to be very infertile, is probably attributable to their ability to accumulate nitrogen and phosphorus, and so enriching the soil. The possibility of growing vegetables in strips ploughed through acacia thickets should be investigated.

ACKNOWLEDGMENTS

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APPENDIX 1A
Site and stand characteristics of exotic acacia thickets in the southern Cape

Locality	Geo- graphical co-ordinates	Distance from sea (km)	Soil texture	Stand age (years)	Stand height (m)	Canopy cover (%)	Cover by other spp. ^a (%)	Plot area (m ²)	Acacia spp.
Hout Bay	34 18 AB	6,0	clay	0,75	0,25	85	1	1	<i>saligna</i> , <i>longifolia</i>
Univ. Cape Town 1 ..	33 18 CD	6,0	clay	2	2,50	80	30	1	<i>longifolia</i> , <i>melanoxylon</i>
Univ. Cape Town 2 ..	33 18 CD	6,0	clay	15	6,00	40	5	25	<i>longifolia</i>
Cape Point	34 18 AD	0,5	sand	4	5,00	90	1	75	<i>saligna</i>
Rondevlei 1	34 18 AB	4,5	sand	35	7,00	70	1	100	<i>cyclops</i> , <i>saligna</i>
Rondevlei 2	34 18 AB	4,5	sand	35	7,00	55	4	25	<i>cyclops</i>
Faure 1	34 18 BA	4,5	sand	35	7,00	60	2	100	<i>cyclops</i> , <i>saligna</i>
Faure 2	34 18 BA	7,5	sand-loam	8	7,00	30	3	25	<i>saligna</i>
Penhill 1	33 18 DD	9,0	sand-loam	10	7,00	30	11	25	<i>saligna</i>
Penhill 2	33 18 DD	9,0	sand-loam	10	7,00	70	10	25	<i>saligna</i>
Marina da Gama	34 18 AB	1,0	sand	5	9,00	85	5	25	<i>cyclops</i> , <i>saligna</i>
Bredasdorp 1	34 20 CA	5,0	lime sand	730	5,50	55	22	50	<i>cyclops</i>
Bredasdorp 2	34 20 CA	5,0	lime sand	730	7,00	70	9	50	<i>cyclops</i>
Goukamma 1	34 22 BB	2,0	sand	35	8,00	55	1	25	<i>cyclops</i> , <i>saligna</i>
Goukamma 2	34 22 BB	2,0	sand	35	6,00	80	1	25	<i>cyclops</i> , <i>saligna</i>

^a Percentage projected cover of plot area

APPENDIX 2

Regression equations for *A. cyclops* and *A. saligna* trees
in the south western Cape

- a: total dry mass on stem diameter (log g/log mm)
b: wood dry mass on stem diameter (log g/log mm)
c: twig dry mass on stem diameter (log g/log mm)
d: foliage dry mass on stem diameter (log g/log mm)

A. cyclops (Faure)

- a: $\log y = -0,61 + 2,54 \log x$ SE(y) = 0,24 r = 0,979
b: $\log y = -1,94 + 3,08 \log x$ SE(y) = 0,30 r = 0,991
c: $\log y = -0,16 + 2,03 \log x$ SE(y) = 0,20 r = 0,925
d: $\log y = -1,40 + 2,52 \log x$ SE(y) = 0,24 r = 0,980

A. saligna (Faure: continuous lines)

- a: $\log y = -1,42 + 2,82 \log x$ SE(y) = 0,16 r = 0,988
b: $\log y = -1,61 + 2,85 \log x$ SE(y) = 0,16 r = 0,995
c: $\log y = -1,87 + 2,67 \log x$ SE(y) = 0,16 r = 0,934
d: $\log y = -3,12 + 3,17 \log x$ SE(y) = 0,19 r = 0,951

A. saligna (Cape Point: dashed line)

- a': $\log y = 0,59 + 1,76 \log x$ SE(y) = 0,14 r = 0,961

APPENDIX 3

Mean wet and dry biomass distribution in above-ground parts of *A. cyclops* and *A. saligna* trees (50–160 mm diameter) in the south western Cape (standard error in parentheses).

WET MASS

	<i>A. cyclops</i> (Faure)	<i>A. saligna</i> (Faure)	<i>A. saligna</i> (Cape Point)
Site	7	7	6
% wood & bark	54,3 (1,2)	63,6 (2,4)	42,8 (3,9)
% brown twigs	24,7 (2,2)	20,5 (1,7)	57,4 (4,0)
% browse (foliage & pods) ...	20,7 (3,0)	16,0 (1,2)	
pods as % of browse Feb.-			
July	14,5 (0,9) ²	0,0 (0,0) ²	0,0 (0,0)
pods as % of browse Nov. ...	62,6 ¹	26,4 ¹	—

DRY MASS

% wood & bark	57,1 (3,6)	72,3 (2,1)	—
% brown twigs	27,5 (3,0)	18,0 (1,5)	—
% browse	15,7 (2,2)	8,5 (1,5)	—
pods as % of browse Feb.-			
July	25,9 (2,0) ²	0,0 (0,0) ²	—
pods as % of browse Nov. ...	63,4 ¹	18,9 ¹	—

1: n = 1

2: n = 2

Analysis of variance for allocation of above-ground biomass

A. cyclops vs. *A. saligna*

Source of variance	SS	DF	MS	F	Signif.
% wood fresh mass					
treatment	301,8	1	301,8	5,51	P = 0,05
error	657,7	12	54,8		
total	959,5	13			
% wood dry mass					
treatment	808,7	1	808,7	13,30	P = 0,01
error	729,6	12	60,8		
total	1 538,3	13			
% twig fresh mass					
treatment	61,8	1	61,8	2,26	ns
error	328,1	12	27,3		
total	399,9	13			
% twig dry mass					
treatment	317,8	1	317,8	8,07	P = 0,05
error	472,3	12	39,4		
total	789,3	13			
% browse fresh mass					
treatment	87,0	1	87,0	2,10	ns
error	496,8	12	41,4		
total	583,8	13			
% browse dry mass					
treatment	117,7	1	117,7	5,70	P = 0,05
error	249,8	12	20,8		
total	367,5	13			

Cape Point vs. *Faure*

% wood fresh mass					
treatment	1 396,2	1	1 396,2	21,99	P = 0,01
error	698,0	11	63,5		
total	2 094,2	12			
% browse & twig fresh mass					
treatment	1 406,8	1	1 406,8	21,64	P = 0,01
error	715,4	11	65,0		
total	2 122,2	12			

THE IDENTITY OF *HYMENOPHYLLUM MARLOTHII* BRAUSE

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ABSTRACT

The identity of *Hymenophyllum marlothii* Brause is discussed and a combination proposed.

UITTREKSEL

Die identiteit van *HYMENOPHYLLUM MARLOTHII* BRAUSE

Die identiteit van *Hymenophyllum marlothii* Brause word bespreek en 'n kombinasie voorgestel.

INTRODUCTION

Hymenophyllum marlothii was described by Brause (1912), and is based on a Marloth collection from Skeleton Ravine on Table Mountain, Cape.

Copeland (1938), in his major revision of the family Hymenophyllaceae dispersed the somewhat 650 species into 33 genera. *H. marlothii* Brause was transferred to the genus *Sphaerocionium* C. Presl. Copeland remarked that "here seems to belong also: with branched hairs on the axis and margin; surface naked: *Hymenophyllum aeruginosum* (Poir.) Carm." A combination was never made.

Hymenophyllum aeruginosum (Poir.) Carm. was at that time only known from Tristan da Cunha (S 37° 0' W 12° 0'), but Wace (1961), whose collection was identified by Alston, reported this species also from Gough Island.

Recent collections of this species which were made by the author on Gough Island were compared with material also collected by the author from the type locality of *H. marlothii* Brause. Comparative studies between material from Gough Island (*H. aeruginosum*), Table Mountain (*H. marlothii*), and Tristan da Cunha, determined by Prof. Pichi Sermolli as *Sphaerocionium aeruginosum*, revealed that these taxa are conspecific.

The name *Hymenophyllum aeruginosum* (Poir.) Carm. antedates that of *Hymenophyllum marlothii* Brause and the latter thus goes into synonymy.

SYSTEMATICS

Hymenophyllum aeruginosum (Poir.) Carm. in Trans. Linn. Soc. **12**: 518 (1818). *Trichomanes aeruginosum* Poir. in Lam., Encycl. Méth. Bot. **8**: 76 (1808). Type: from Tristan da Cunha, *M. Bory de Saint-Vincent s.n.* in Herb. du Petit-Thouars (P, holo.).

Hymenophyllum marlothii Brause in Fedde. Repert. **XI**: 112 (1912). Type: from South Africa, Skeleton Ravine, Table Mountain, *Marloth 5169* (B, holo.).

Sphaerocionium marlothii (Brause) Copel. in Philipp. J. Sci. **67**(1): 33 (1938).

Hymenophyllum obtusatum Hk. & Arn. sensu Sim, Ferns of S. Afr. ed. 1, p.49, pl. 6 (1892).

Merely for convenience and the fact that the system proposed by Copeland is not widely accepted the species involved is retained in the genus *Hymenophyllum*. A more natural and acceptable system was proposed by Morton (1968).

The type of *H. aeruginosum*, which was seen by Prof. Pichi Sermolli on May 28, 1967 was determined as *Sphaerocionium aeruginosum* (Poir.) Pic. Serm. but the publication of this name could not be traced by the author.

MATERIAL EXAMINED

SOUTH ATLANTIC—S 37° 0' W 12° 0' (Tristan da Cunha): Middle pond, 575 m, 19/1/1938, *Christophensen 1245* (P); Tristan da Cunha, 1873, *Mosely s.n.*, 1873 (P.).

—S 40° 21' W 9° 53' (Gough Island): Streambanks north-east of meteorological station, *Roux 717* (NBG); South-eastern slopes of Tafel Koppie, *Roux 742* (NBG).

CAPE—3318 (Cape Town): Table Mountain (—CD), *Esterhuysen 12538* (SAM); Wynberg, *Barkly 24414* (SAM); Skeleton Gorge, *Bond 423* (NBG); Top of Nursery Gorge, Table Mountain, *Roux 74* (NBG); Valley of Isolation, Table Mountain, *Esterhuysen 21808* (NBG); Kasteels Poort, Table Mountain, *Froembling 655* (NBG); Skeleton Ravine, Table Mountain, *Roux 779* (NBG, P).

—3322 (Oudtshoorn): George (—CD), *Shaw 1881* (SAM).

—3323 (Willowmore): Joubertina, ravine (—DD), *Esterhuysen 7081* (NBG).

—3420 (Bredasdorp): In kloof on southern slopes of Langebergen near Heidelberg (—BB), *Esterhuysen 14449* (NBG).

—3423 (Knysna): Knysna (—AA), *Rex s.n.* (SAM).

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PHYTOGEOGRAPHIC AND BIOTIC RELATIONSHIPS OF A SAVANNA IN SOUTHERN AFRICA: ANALYSIS OF AN ANGIOSPERM CHECK-LIST FROM ACACIA WOODLAND IN ZULULAND

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ABSTRACT

Floristic analysis of a list of 425 species revealed some ecological features of a semi-arid woodland or savanna represented in the Umfolozi Game Reserve, which is dominated by *Acacia* species and graminoid forms. A poor representation of forbs was ascribed to foraging and trampling by indigenous herbivores. An exceptionally low presence of species of Orchidaceae and Asclepiadaceae was apparently due in part to elimination of their insect pollinators when DDT was applied to control tse-tse flies some 30 years ago. The Reserve is evidently close to the southernmost limit of *Acacia* Woodland of the Zambezi Domain. The Reserve contains many species of Tiliaceae and Ebenaceae characteristic of the Tongaland-Pondoland Regional Mosaic, but few species are present from other phytochoria in the Indian Ocean Coastal Belt.

UITTREKSEL

FITOGEOGRAFIESE EN BIOTIESE VERHOUDINGS VAN 'N SAVANNA IN SUIDELIKE AFRIKA: ANALISE VAN 'N ANGIOSPERM KONTROLELYS VAN 'N ACACIA-BOSLAND IN ZOELOELAND

'n Floristiese analise van 425 spesies onthul 'n paar ekologiese kenmerke van 'n semi-droë bosland of savanna, wat deur *Acacia* spesies en grasagtige plante gedomineer word. Kruide was swak verteenwoordig en dit word toegeskryf aan beweidings en uittrapping deur inheemse plantvreters. 'n Besondere lae persentasie spesies van die Orchidaceae en Asclepiadaceae kan gedeeltelik toegeskryf word aan die eliminering van hul insekbestuiers toe DDT aangewend is om tsetsevlies te beheer. Die Reservaat kom voor as 'n unieke, mees suidelike grens van *Acacia*-bosland wat tipies is van die Zambesie Gebied. Die Reservaat bevat baie soorte Tiliaceae en Ebenaceae wat kenmerkend is van die Tongaland-Pondoland streeks-mosaiek, maar min verteenwoordigers uit ander gebiede van die Indiëroseaan kus-streek word ontdek.

INTRODUCTION

The Umfolozi Game Reserve was selected for this phytogeographic study because its area of 500 km² contains the most extensive, diverse and well-preserved representative of semi-arid savanna found on the eastern seaboard of South Africa. The Reserve was proclaimed in 1897 in order to protect wildlife in

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the vicinity of the confluence of the Black and White Mfolozi Rivers, which lies near latitude S 28° 20', longitude E 31° 50', at a point 50 km west of where Lake St Lucia opens to the Indian Ocean. Proclaimed in 1897, the Umfolozi is one of the early nature reserves established in Africa. Vegetation in the Reserve is in a good state of preservation compared with similar areas of savanna used by farmers.

The Reserve is markedly different from immediately adjacent areas in both climate and vegetation. The Reserve itself is hot and dry, as reflected by a mean annual temperature of 23 °C and a mean annual rainfall of 635 mm. These semi-arid conditions arise because the Reserve lies within the valleys of the Black and White Mfolozi Rivers which are deeply incised.

The valleys differ from the cooler and more humid climate of adjacent highlands to the north and west. The highland vegetation is grassland and forest of a more temperate nature, and contrasts with an obviously xerophytic, largely spinescent and deciduous *Acacia* Woodland in the dry valleys of the Reserve. There is another sharp contrast with yet a third bioclimatic region to the east of the Reserve. Some 20 km east of the confluence, the Mfolozi River enters the hot and humid Zululand Coast Plain which has tropical evergreen vegetation.

A main purpose of this study is to record the angiosperm species in the Reserve, an important objective in view of the rapid deterioration of other areas of *Acacia* habitat. Although valleys geomorphologically similar to the Mfolozi exist to the south (for example the Tugela and the Mkomazi) the vegetation of these areas has been radically altered by human activity. The study also attempts an explanation of some interesting phytogeographical aspects of vegetation in the Reserve which provides food or shelter for some 18 species of large herbivores. Names and biomasses of these animals are available from Mentis (1970).

METHOD

The basic list of species was compiled from plant collections made by Downing during the course of a detailed plant ecological study (Downing, 1972). Sets of specimens are housed at herbaria in Hluhluwe Game Reserve, the University of Natal in Pietermaritzburg (NU) and at the Botanical Research Institute in Pretoria (PRE).

RESULTS

A total of 425 species or subspecific taxa are listed for the Reserve in the Appendix. These species are distributed into higher taxa as shown in Table 1. All families with five or more species (more than one percent of the total number of species) are listed in Table 2.

Comparison between the largest families in the Reserve with the largest families from other areas in southern Africa show some interesting differences.

TABLE 1.

Numbers of taxa represented in the check-list of angiosperms of the Umfolozi Game Reserve.

	Monocotyledonae		Dicotyledonae		Total
	No.	% of total	No.	% of total	
Families	10	11,7	76	88,4	86
Genera	77	30,1	179	69,9	256
Species	154	36,2	271	63,8	425

TABLE 2.

Families with more than 1 % of the total number of species.

Family	No. species	% of total no. of spp. (425)	No. genera	% of total no. of genera (256)
1. Gramineae	103	24,3	49	19,2
2. Leguminosae	30	7,0	15	5,9
3. Compositae	28	6,6	18	7,1
4. Cyperaceae	23	5,4	7	2,7
5. Acanthaceae	16	3,8	11	4,3
6. Liliaceae	15	3,5	10	3,9
7. Euphorbiaceae	12	2,8	9	3,5
8. Rubiaceae	11	2,6	7	2,7
9. Tiliaceae	10	2,4	1	0,4
10. Ebenaceae	9	2,1	2	0,8
11. Anacardiaceae	7	1,7	3	1,2
12. Moraceae	7	1,7	1	0,4
13. Malvaceae	6	1,4	5	2,0
14. Boraginaceae	6	1,4	4	1,6
15. Capparaceae	6	1,4	4	1,6
16. Celastraceae	6	1,4	2	0,8
17. Amaranthaceae	5	1,2	5	2,0
18. Labiatae	5	1,2	5	2,0
19. Vitaceae	5	1,2	3	1,2
20. Sterculiaceae	5	1,2	3	1,2

Generally, the major components of the floras of all these areas are much the same even though the sizes of the areas vary considerably both in extent and in number of species, as shown in Table 3. Note that in all lists the Leguminosae, Compositae and Gramineae are in the positions of the three largest families. Furthermore, all five lists have the families Rubiaceae, Cyperaceae and Liliaceae; four of the lists have Euphorbiaceae and Asclepiadaceae; three of the lists have Acanthaceae; two of the lists have Scrophulariaceae and Labiatae.

TABLE 3.

The number of species contained by the 10 largest families in the Umfolozi Game Reserve compared with the 10 largest families in four other areas. Data for Suikerbosrand Nature Reserve from Bredenkamp and Lamprechts (1979), and from Gibbs Russell (1975) for the remainder.

Umfolozi G.R.	Suikerbosrand N.R.	Natal	Swaziland	Rhodesia
Gramineae	103	Compositae	Compositae	Leguminosae
Leguminosae	30	Leguminosae	Leguminosae	Gramineae
Compositae	28	Gramineae	Gramineae	Compositae
Cyperaceae	23	Liliaceae	Liliaceae	Orchidaceae
Acanthaceae	16	Asclepiadaceae	Asclepiadaceae	Orchidaceae
Liliaceae	15	Cyperaceae	Labiatae	Cyperaceae
Euphorbiaceae	12	Scrophulariaceae	Orchidaceae	Euphorbiaceae
Rubiaceae	11	Asclepiadaceae	Euphorbiaceae	Rubiaceae
Tiliaceae	10	Rubiaceae	Orchidaceae	Asclepiadaceae
Ebenaceae	9	Acanthaceae	Cyperaceae	Liliaceae
		Labiatae	Rubiaceae	Acanthaceae
		Scrophulariaceae		
No. spp. in 10 largest families	257	546	260	610
Total no. spp. in flora	425	420	220	563
% of total no. spp. in 10 largest families . . .	61	410	173	372
Area covered (km ²) . . .	500	226	137	353
		207	104	224
		206	103	192
		168	84	177
		146	82	163
		130	76	159
		127	70	158
		2 586	1 309	2 971
		4 818	2 307	5 204
		54	57	57
		86 967	17 363	390 750

Only one of the lists, that of the Umfolozi Game Reserve, has families ranked among the ten largest that occur only on that one list. These are the families Tiliaceae and Ebenaceae. Conversely, only in the flora of the Reserve are the Orchidaceae and Asclepiadaceae missing from the list of largest families. (In the Suikerbosrand Nature Reserve, the Orchidaceae is in 12th position in number of species.)

DISCUSSION

Biotic and climatic factors may explain the near absence of members of Orchidaceae from the Reserve, even though they are important in the floras of adjacent regions. Ground orchids are unknown in the Reserve, even though species occur in other dry areas. It is suggested that several biotic factors may have caused their elimination from the Reserve by reducing both their asexual and sexual means of propagation.

Game animals such as warthog, wild pig, porcupine, baboon and antelopes, which feed on the underground storage organs of plants, are present in the Reserve in heavy concentrations. During the winter months when succulent herbage is very scarce they could have severely depleted the rhizomes of any ground orchids present, thus impairing their asexual propagation. At the same time, sexual reproduction could have been inhibited by elimination of insect pollinators as a result of the extensive and intensive spraying of insecticides (DDT and BHC) during the anti-nagana or tse-tse fly campaign in the Reserve from 1947 to 1951 (see Vincent, 1970). Orchids would be especially sensitive to such a loss of pollinators because of the close co-evolution of orchid and hymenopteran species.

The lack of epiphytic orchids is probably also a response to the insecticides as well as to climatic conditions. The greatest concentration of epiphytic orchids in South Africa is in Zululand, mainly in the magisterial districts of Eshowe, Hlabisa and Ingwavuma (Harrison, 1972). These districts are for the greater part much more humid than the arid Reserve which they virtually surround. Thus, dry atmospheric conditions in the Reserve may have precluded a high representation of epiphytic orchids. The only species recorded, *Ansellia gigantea*, is well known from dry areas. The species appears to be represented in the Reserve by a single colony of great age, and no young specimens were found. This suggests that reproduction has been adversely affected in the epiphytic orchids. Surprisingly, the small orchid *Microcoelia exilis* has not been recorded for the Reserve even though it is an abundant epiphyte on some *Acacia* thickets in the Hluhluwe, Mkuze, and St Lucia Reserves.

The paucity of Asclepiadaceae might also be a result of elimination of pollinating insects, damage by herbivores and damage from periodic veld fires.

Furthermore, both Orchidaceae and Asclepiadaceae are mostly herbaceous families and their paucity is part of an overall scarcity of forbs in the Reserve.

This scarcity is probably due to a selective-grazing habit of the herbivores, detailed by Downing (1974, 1979), whereby some areas are grazed lightly whilst others are heavily grazed and trampled. A typical, lightly grazed stand could have an 800 mm tall layer of grasses with a canopy cover of 60 %. Competition from so dense a stand of tall grasses is such that the cover of short forbs is confined to one or two percent. The forbs are mostly of a woody nature and are fire sensitive. Fires, which easily burn through such stands after drying of the grasses in winter, also suppress the forb growth. However, in over-grazed areas the grasses are reduced to a height of 200 mm and a canopy cover of 15 % or less; the passage of fire is not possible in such conditions in the Reserve and forb cover increases to 25 %. Although forb density is relatively high in these over-grazed areas, the plants represent only a few, prolific species. These are often annuals from the families Compositae and Acanthaceae, the latter being rather well represented in the Reserve (see Table 3). The annuals survive intensive trampling by animal hooves, induration of the bare soil surface by exposure to insolation, and reduced soil-water infiltration consequent to overgrazing.

The two families which replace the Orchidaceae and Asclepiadaceae among the ten largest families in the Reserve are the Ebenaceae and Tiliaceae (Table 3). Ebenaceae is prominent in the flora because of the large number of species in the genera *Euclea* and *Diospyros*. White and Moll (1978) state that these two genera have their centres of distribution in the Tongaland-Pondoland Regional Mosaic of the Indian Ocean Coastal Belt. The Reserve contains nine members of the Ebenaceae and may thus be of some importance for evolutionary study of this family. Much the same could be said of the Tiliaceae which is represented by 10 species of *Grewia*.

TABLE 4.
Genera with more than 1 % of the total number of species.

Genus	No. spp.	% of total no. of species (425)
<i>Acacia</i>	14	3,3
<i>Cyperus</i>	10	2,4
<i>Grewia</i>	10	2,4
<i>Digitaria</i>	9	2,1
<i>Brachiaria</i>	8	1,9
<i>Sporobolus</i>	8	1,9
<i>Aristida</i>	7	1,7
<i>Eragrostis</i>	7	1,7
<i>Ficus</i>	7	1,7
<i>Euclea</i>	5	1,2
<i>Scirpus</i>	5	1,2

All of the 11 genera in the Reserve which have more than one percent of the total number of species (Table 4) are either woody or graminoid in habit. This reflects the physiognomic essence of vegetation structure in the Reserve, which is a 5 m tall layer of conspicuous trees imposed upon a grass layer. Occasionally, where shrubs are dense, they may form a distinct stratum. The two largest genera show specific adaptations to the seasonally arid conditions. *Acacia* in the Reserve has finely divided deciduous leaves which are supposed to fold during unseasonal drought and which are shed during the regular, winter droughts. *Cyperus* often has hard underground storage organs and, like all other plants of graminoid habit in the Reserve, undergoes die-back of the aerial portions during the dry winter months.

That the Reserve may be near the southern limit of *Acacia* Woodlands is indicated because a number of species in the largest woody genera (Table 4) are at or near the limits of their distribution. For the 14 species of *Acacia* in the Reserve, Ross (1971) shows that the Reserve is at the southernmost limit for the distribution of four species (*Acacia borleae*, *A. grandicornuta*, *A. luederitzii* var. *retinens*, and *A. nigrescens*), while another eight species are near the southern limit of their distribution. Furthermore, two species (*A. davyi* and *A. xanthophloea*) have a distribution which ends just north of the Reserve near Hluhluwe.

Some species of *Grewia*, *Ficus* and *Euclea* are shown in the maps of Coates Palgrave (1978) to also have their southern distribution limits near the Reserve. Of the 10 species of *Grewia* recorded in the Reserve, seven (*Grewia bicolor*, *G. caffra*, *G. flava*, *G. flavescens*, *G. hexamita*, *G. subspathulata* and *G. villosa*) are near the southern limits of their distribution. *Ficus* has four (*Ficus capreifolia*, *F. pretoriae*, *F. stuhlmannii* and *F. sycamorus*) of its seven species near the distribution limits. *Euclea* has five species recorded in the Reserve, of which two (*Euclea divinorum* and *E. undulata*) extend no farther to the south in Natal.

The area of the Reserve is included by White & Moll (1978) as part of their Tongaland-Pondoland Regional Mosaic in the Indian Ocean Belt. However, the Reserve might be more closely related to the Zambezan Region than to any other region of the Indian Ocean Belt. Of the 15 endemic genera listed by White & Moll for the Tongaland-Pondoland Regional Mosaic, only two, *Hippobromus* and *Galpinia*, occur in the Reserve. A link between the Tongaland-Pondoland Mosaic and the Reserve is the large number of species of Ebenaceae; but both *Euclea* and *Diospyros* are widespread genera with many species in Zimbabwe and Botswana, which both lie in the Zambezan Region.

Relationships between the flora of the Reserve and other major phytochoria of Southern Africa are summarized in Table 5. Some fairly strong affinities are shown between the Reserve and the Zambezan Region, and to a lesser extent the Karoo-Namib Region; but there is little similarity to other phytochoria. Physiognomically the vegetation of the Indian Ocean Coastal Belt is typically forest whereas the Zambezan Domain is typically savanna or woodland (Werger,

TABLE 5.

Total number of species, quoted by White & Moll (1978) as linking the Tongaland-Pondoland with other phytochoria, as compared with the numbers of these species recorded in Umfolozi Game Reserve.

Phytochorion	No. of linking species quoted by White & Moll (1978)	No. of these species occurring in the Reserve
Zambezian	26	5
Afromontane	5	0
"Upland"	14	0
Cape/Afromontane	8	0
Karoo-Namib	12	3
Guineo-Congolian	9	1

1978). In this regard also the Reserve appears to have closer affinities with the Zambezian Region.

CONCLUSIONS

The flora of the Reserve is regarded as a discrete section of the Tongaland-Pondoland Regional Mosaic that is characterised by strong Zambezian affinities, but which has few affinities with adjacent phytochoria, including the northern region of the Indian Ocean Coastal Belt. This lack of floristic similarity with surrounding, comparatively humid areas (whether of highland or coast plain) is expected in view of the marked physiographic and climatic differences between the deeply incised Mfolozi valley and contiguous areas.

The Reserve is situated close to the distribution limit of many *Acacia* species and could be regarded as the southernmost extension of the *Acacia* Woodlands or Savannas typical of parts of central and east Africa. Nowhere south of the Reserve is found such a diversification and dominance by *Acacia* species.

The possibility of Orchidaceae and Asclepiadaceae having being reduced through elimination of insect pollinators cannot easily be confirmed because no check-list of the flora was available prior to the present, and very few or no botanical records were made for the Reserve prior to the aerial spraying of insecticides starting in 1948. Reference to proximal, geographically similar areas might help resolve the problem even though being of farmland or of conserved areas similarly treated with insecticides. Rather similar floral types to Umfolozi are in lowlands to the north, e.g. near Hluhluwe and Mkuze, but these appear less comprehensive and are extensively disturbed by human activity.

In spite of the use of insecticides and of other interference, the extent of the Reserve warrants conservation because its vegetation appears to be the last,

reasonably intact and comprehensive representative of what is probably a unique floral type close to the southernmost limit of its distribution in south-east Africa.

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APPENDIX: SYSTEMATIC LIST

Angiosperm families and genera appear in the order used in *The Flora of Natal* (Ross, 1972). Species are listed alphabetically within genera. Aquatic plants and exotics are excluded. Additional species records are most likely to be obtained near rock outcrops and stream banks. The majority of species listed can be

found in many of ten woody plant communities mapped and floristically described in detail by Downing (1972). The major differences between these communities lay in differences, sometimes of only minor magnitude, in the relative abundance of species present. Provision of detailed habitat data in the check-list thus seems of little value. However, a notation in the margin by the letters O (for Open Woodland), C (for Closed Woodland) or R (for Riverine Woodland) is given only for those species with a conspicuous preference for a particular woodland association. The collection numbers of Downing are cited in the list. Absence of a number indicates that the record was obtained from a specimen in some other collection at the Hlululuwe Herbarium.

GRAMINEAE

<i>Imperata cylindrica</i> (L.) Beauv. var. <i>major</i> (Nees) C. E. Hubb.	583	R
<i>Ischaemum arcuatum</i> (Nees) Stapf	542	R
<i>Hemarthria altissima</i> Stapf & C. E. Hubb.	540	R
<i>Trachypogon spicatus</i> (L.f.) Kuntze		
<i>Elyonurus argenteus</i> Nees	438	
<i>Andropogon appendiculatus</i> Nees		
<i>Sorghum halepense</i> (L.) Pers.	470	R
<i>Bothriochloa insculpta</i> (Hochst.) A. Camus	565	
<i>Cymbopogon excavatus</i> (Hochst.) Stapf ex Burtt Davy		
<i>Cymbopogon marginatus</i> (Steud.) Stapf ex Burtt Davy	567	
<i>Cymbopogon plurinodis</i> (Stapf) Stapf ex Burtt Davy	580	
<i>Cymbopogon validus</i> Stapf ex Burtt Davy		
<i>Hyparrhenia filipendula</i> (Hochst.) Stapf var. <i>pilosa</i> (Hack.) Stapf	566	
<i>Hyparrhenia hirta</i> (L.) Stapf	578	
<i>Heteropogon contortus</i> (L.) Beauv. ex Roem. & Schult.	477	
<i>Diheteropogon amplexans</i> (Nees) W. D. Clayton	526	
<i>Hyperthelia dissoluta</i> (Nees ex Steud.) W. D. Clayton	571	O
<i>Themeda triandra</i> Forsk. var. <i>trachyspathea</i> Goosens	428	O
<i>Tragus berteronianus</i> Schult.	444	C
<i>Perotis patens</i> Gand.	445	
<i>Paspalum commersonii</i> Lam.	626	R
<i>Paspalum distichum</i> L.	627	R
<i>Paspalidium</i> sp.		
<i>Eriochloa borumensis</i> Stapf		
<i>Panicum coloratum</i> L.		C
<i>Panicum deustum</i> Thunb.	425	C
<i>Panicum maximum</i> Jacq.	471	C
<i>Panicum meyerianum</i> Nees var. <i>grandeglume</i> Stent & Rattray	615	R
<i>Urochloa mosambicensis</i> (Hack.) Dandy	441	C
<i>Urochloa trichopus</i> (Hochst.) Stapf	524	
<i>Brachiaria deflexa</i> (Schum.) C. E. Hubb. ex Robyns	468	
<i>Brachiaria dictyoneura</i> (Fig. & de Not.) Stapf	525	
<i>Brachiaria eruciformis</i> (Sibth. & Smith) Griseb.	520	
<i>Brachiaria humicola</i> (Rendle) Schweick.		
<i>Brachiaria nigropedata</i> (Munro) Stapf	434	
<i>Brachiaria ramosa</i> Stapf		
<i>Brachiaria serrata</i> (Spreng.) Stapf		
<i>Brachiaria xantholeuca</i> (Hack.) Stapf		
<i>Echinochloa colonum</i> (L.) Link.	581	R
<i>Echinochloa holubii</i> (Stapf) Stapf		R

<i>Sacciolepis curvata</i> (L.) Chase	
<i>Digitaria argyrograptia</i> (Nees) Stapf	521 C
<i>Digitaria debilis</i> (Desf.) Willd.	
<i>Digitaria eriantha</i> Steud.	
<i>Digitaria longiflora</i> (Retz.) Pers.	523
<i>Digitaria macroglossa</i> Henrard	501a
<i>Digitaria natalensis</i> Stent	
<i>Digitaria pentzii</i> Stent	
<i>Digitaria polevansii</i> Stent	519 C
<i>Digitaria smutsii</i> Stent	467 C
<i>Tricholaena monachne</i> (Trin.) Stapf & C. E. Hubb.	508
<i>Rhynchelytrum repens</i> (Willd.) C. E. Hubb.	415
<i>Rhynchelytrum villosum</i> (Parl.) Chiov.	582
<i>Setaria perennis</i> Hack.	448
<i>Setaria sphacelata</i> (Schumach.) Stapf & C. E. Hubb. ex M. B. Moss	522
<i>Setaria verticillata</i> (L.) Beauv.	564
<i>Setaria woodii</i> Hack.	439 O
<i>Cenchrus ciliaris</i> L.	514
<i>Aristida adsencionis</i> L.	
<i>Aristida bipartita</i> (Nees) Trin. & Rupr.	511
<i>Aristida congesta</i> Roem. & Schult. ssp. <i>barbicollis</i> (Trin. & Rupr.) de Winter	576
<i>Aristida congesta</i> Roem. & Schult. ssp. <i>congesta</i>	575
<i>Aristida diffusa</i> Trin. var. <i>burkei</i> (Stapf) Schweick.	572
<i>Aristida scabrivalvis</i> Hack.	
<i>Aristida stipitata</i> Hack. ex Schinz var. <i>graciliflora</i> (Pilg.) Melderis	577
<i>Sporobolus festivus</i> Hochst. ex A. Rich.	
<i>Sporobolus fimbriatus</i> Nees var. <i>fimbriatus</i>	
<i>Sporobolus fimbriatus</i> Nees var. <i>latifolia</i> Stent	503a
<i>Sporobolus nitens</i> Stent	440 C
<i>Sporobolus pyramidalis</i> Beauv.	579
<i>Sporobolus smutsii</i> Stent	437
<i>Sporobolus stapfianus</i> Gandoger	420
<i>Sporobolus virginicus</i> (L.) Kunth	
<i>Apochaete hispida</i> (L.f.) Phipps	
<i>Cynodon dactylon</i> (L.) Pers.	443
<i>Harpechloa falx</i> (L.) Kuntze	
<i>Enteropogon monostachyos</i> (Vahl) K. Schum. ssp. <i>africanus</i> W. D. Clayton	423
<i>Chloris gayana</i> Kunth	541
<i>Chloris pycnothrix</i> Trin.	539
<i>Chloris virgata</i> Sw.	513
<i>Eustachys paspaloides</i> (Vahl) Lanza & Mattei	466
<i>Tripogon abyssinicus</i> Nees	
<i>Tetrapogon mosambicensis</i> (K. Schum.) L. Chippindall ex B. S. Fisher	518
<i>Eleusine indica</i> (L.) Gaertn. f.	538
<i>Dactyloctenium australe</i> Steud.	509
<i>Dactyloctenium giganteum</i> Fischer & Schweick.	515
<i>Leptochloa panicea</i> (Retz.) Ohwi	563
<i>Enneapogon cenchroides</i> (Licht.) C. E. Hubb.	506
<i>Enneapogon scoparius</i> Stapf	465
<i>Fingerhuthia africana</i> Lehm.	544
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	
<i>Phragmites mauritianus</i> Kunth	651 R
<i>Diplachne eleusine</i> Nees	433
<i>Diplachne fusca</i> (L.) Beauv. ex Stapf	
<i>Pogonarthria squarrosa</i> (Licht.) Pilg.	504
<i>Trichoneura grandiglumis</i> (Nees) Ekman	419

<i>Eragrostis barbinodis</i> Hack.	507
<i>Eragrostis cilianensis</i> (All.) Lutati	547
<i>Eragrostis ciliaris</i> (L.) R. Br.	628
<i>Eragrostis curvula</i> (Schrad.) Nees	416
<i>Eragrostis gummiflua</i> Nees	549
<i>Eragrostis heteromera</i> Stapf	510
<i>Eragrostis superba</i> Peyr.	417

CYPERACEAE

<i>Cyperus articulatus</i> L.	629
<i>Cyperus difformis</i> L.	562
<i>Cyperus leptocladus</i> Kunth	436
<i>Cyperus margaritaceus</i> Vahl	435
<i>Cyperus fastigiatus</i> Rottb.	
<i>Cyperus obtusiflorus</i> Vahl	449
<i>Cyperus rupestris</i> Kunth	620
<i>Cyperus sexangularis</i> Nees	616
<i>Cyperus teneriffae</i> Poir.	421
<i>Cyperus textilis</i> Thunb.	
<i>Mariscus indecorus</i> (Kunth) Podlech	423
<i>Mariscus sieberianus</i> Nees	
<i>Mariscus vestitus</i> C.B. Cl.	619
<i>Kyllinga erecta</i> Schumach.	422
<i>Kyllinga melanosperma</i> Nees	
<i>Scirpus articulatus</i> L.	
<i>Scirpus cernuus</i> Vahl	
<i>Scirpus muricinix</i> C.B. Cl.	
<i>Scirpus paludicola</i> Kunth	
<i>Scirpus praelongatus</i> Poir.	
<i>Fimbristylis hispidula</i> (Vahl) Kunth	463
<i>Fimbristylis ovata</i> (Burm. f.) Kern	
<i>Bulbostylis boeckleriana</i> (Schweinf.) Beetle	424

PALMAE

<i>Phoenix reclinata</i> Jacq.	R
<i>Hyphaenae natalensis</i> Kuntze	R

COMMELINACEAE

<i>Commelina africana</i> L.	533
<i>Commelina benghalensis</i> L.	536
<i>Murdannia simplex</i> (Vahl) Brenan	617

JUNCACEAE

<i>Juncus lomatophyllus</i> Spreng.	R
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LILIACEAE

<i>Bulbine natalensis</i> Bak	
<i>Anthericum galpinii</i> Bak.	600
<i>Eriosperrum burchellii</i> Bak.	

<i>Eriospermum galpinii</i> Schinz	
<i>Aloe marlothii</i> Berger	
<i>Aloe vanbalenii</i> Pillans	
<i>Gasteria</i> sp.	
<i>Albuca pachychlamys</i> Bak.	
<i>Dipcadi gracillima</i> Bak.	
<i>Scilla</i> sp.	604
<i>Ornithogalum ecklonii</i> Schlecht.	
<i>Asparagus falcatus</i> L.	
<i>Asparagus macowanii</i> Bak. var <i>zuluensis</i> (N.E. Br.) Jessop	
<i>Asparagus subulatus</i> Thunb.	
<i>Asparagus virgatus</i> Bak.	550

AMARYLLIDACEAE

<i>Haemanthus multiflorus</i> Mart.
<i>Ammocharis coranica</i> (Ker-Gawl.) Herb.
<i>Cyrtanthus galpinii</i> Bak.

IRIDACEAE

<i>Anomatheca laxa</i> (Thunb.) Goldblatt

MUSACEAE

<i>Strelitzia reginae</i> Banks ex Ait.

ORCHIDACEAE

<i>Ansellia gigantea</i> Reichb. f. var. <i>nilotica</i> Summerh.

SALICACEAE

<i>Salix woodii</i> Seemen	R
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ULMACEAE

<i>Chaetacme aristata</i> Planch.

MORACEAE

<i>Ficus capensis</i> Thunb.	
<i>Ficus capreifolia</i> Del.	
<i>Ficus pretoriae</i> Burt Davy	596
<i>Ficus soldanella</i> Warb.	
<i>Ficus sonderi</i> Miq.	589
<i>Ficus stuhlmannii</i> Warb.	487 O
<i>Ficus sycomorus</i> L.	595 R

URTICACEAE

<i>Urera tenax</i> N.E. Br.

LORANTHACEAE

Loranthus kraussianus Meisn.*Loranthus natalitus* Meisn.*Loranthus ngamicus* Sprague

SANTALACEAE

Thesium resedoides A.W. Hill

OLACACEAE

Ximenia caffra Sond. var. *natalensis* Sond.

POLYGONACEAE

Polygonum salicifolium Willd.

CHENOPODIACEAE

Chenopodium album L.

558

AMARANTHACEAE

Cyphocarpa angustifolia Lopr.

529

Cyathula spathulifolia Lopr.*Achyroopsis leptostachya* Hook.f.*Alternanthera repens* (L.) O. Kuntze*Gomphrena celosioides* Mart.

601

NYCTAGINACEAE

Boerhavia diffusa L.

MOLLUGINACEAE

Hypertelis salsoloides (Burch.) Adamson

AIZOACEAE

Aizoon canariense L.*Aizoon glinoides* L.f.

543

MESEMBRYANTHEMACEAE

Aptenia cordifolia (L.f.) N.E. Br.

537

Delosperma pachyrhizum L. Bol.

PORTULACACEAE

Portulacaria afra Jacq.*Portulaca kermesina* N.E. Br.

537b

Portulaca quadrifida L.

610

CARYOPHYLLACEAE

Dianthus zeyheri Sond. ssp. *natalensis* Hooper

O

CERATOPHYLLACEAE

Ceratophyllum demersum L.

MENISPERMACEAE

Cissampelos mucronata A. Rich.

CAPPARACEAE

Cleome diandra Burch.

Cleome monophylla L.

Capparis tomentosa Lam.

Boscia albitrunca (Burch.) Gilg & Ben.

Maerua angolensis DC.

649

Maerua rosmarinoides (Gand.) Gilg & Ben.

CRASSULACEAE

Crassula argentea Thunb.

Crassula transvaalensis Kuntze

LEGUMINOSAE

Acacia borleae Burtt Davy

481

Acacia brevispica ssp. *dregeana* (Benth.) Brenan

561

Acacia burkei Benth.

Most specimens in the Reserve are hybrids between *A. burkei* and *A. nigrescens* (Dr J. Ross, pers. comm.).

Acacia caffra (Thunb.) Willd.

O

Acacia gerrardii Benth. var. *gerrardii*

O

Acacia grandicornuta Gerstner

C

Acacia karroo Hayne

451 O

Acacia luederitzii Engl. var. *retinens* (Sim) Ross & Brenan

C

Acacia nigrescens Oliv.

O

Acacia nilotica (L.) Willd. ex Del. ssp. *kraussiana* (Benth.) Brenan

C

Acacia robusta Burch. ssp. *clavigera* (E. Mey.) Brenan

R

Acacia senegal (L.) Willd. var. *rostrata* Brenan

Acacia sieberiana DC. var. *woodii* (Burtt Davy) Keay & Brenan

552

Very rare in the Reserve, known only from Makhamisa area.

Acacia tortilis (Forsk.) Hayne ssp. *heteracantha* (Burch.) Brenan

O

Dichrostachys cinerea (L.) Wight & Arn.

Entada wahlbergii Harv.

597 R

Schotia brachypetala Sond.

Schotia capitata Bolle

479 C

Peltophorum africanum Sond.

Crotalaria monteiroi Taub. ex Bak.f.

Indigofera costata Guill. & Perr.

Indigofera sp. (= Tinley 850)

614

Mundulea sericea (Willd.) A. Chev.

Sesbania bispinosa (Jacq.) W. F. Wight

<i>Ormocarpum trichocarpum</i> (Taub.) Engl.	O
<i>Stylosanthes fruticosa</i> (Retz.) Alston	
<i>Glycine wightii</i> (R. Grah. ex Wight & Arn.) Verdc.	
<i>Erythrina lysistemon</i> Hutch.	592
<i>Rhynchosia nitens</i> Benth	
<i>Vigna decipiens</i> Harv.	605

OXALIDACEAE

Oxalis smithiana Eckl. & Zeyh.

ERYTHROXYLACEAE

<i>Erythroxylum delagoense</i> Schinz	587
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ZYGOPHYLLACEAE

<i>Tribulus terrestris</i> L	534
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BALANITACEAE

Balanites maughamii Sprague

RUTACEAE

Fagara capensis Thunb.

BURSERACEAE

<i>Commiphora harveyi</i> (Engl.) Engl.	
<i>Commiphora neglecta</i> Verdoorn	458
<i>Commiphora pyracanthoides</i> Engl.	
<i>Commiphora schimperi</i> (O. Berg.) Engl.	

MELIACEAE

<i>Turraea obtusifolia</i> Hochst.	586
<i>Trichilia emetica</i> Vahl	

MALPHIGIACEAE

Sphedamnocarpus galphimifolius (A. Juss.) Szyszyl.

POLYGALACEAE

<i>Polygala serpentaria</i> Eckl. & Zeyh.	599
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EUPHORBIACEAE

<i>Securinea virosa</i> (Roxb. ex Willd.) Pax & K. Hoffm.	517
<i>Phyllanthus maderaspatensis</i> L.	603
<i>Croton menyhartii</i> Pax	477
<i>Erythrococca natalensis</i> Prain	

<i>Acalypha glabrata</i> Thunb.	
<i>Acalypha indica</i> L.	557
<i>Tragia meyeriana</i> Muell. Arg.	
<i>Jatropha variifolia</i> Pax	
<i>Spirostachys africana</i> Sond.	C
<i>Euphorbia grandicornis</i> Goebel ex N.E. Br. ssp. <i>grandicornis</i>	C
<i>Euphorbia matabelensis</i> Pax	
<i>Euphorbia tirucalli</i> L.	

ANACARDIACEAE

<i>Sclerocarya caffra</i> Sond.	O
<i>Ozoroa engleri</i> R. & A. Fernandes	591 O
<i>Ozoroa obovata</i> (Oliv.) R. & A. Fernandes	460 O
<i>Ozoroa paniculosa</i> (Sond.) R. & A. Fernandes	640 O
<i>Rhus chirindensis</i> Bak.f. forma <i>legatii</i> (Schonl.) R. & A. Fernandes	584
<i>Rhus gueinzii</i> Sond. var. <i>spinescens</i> (Diels) R. & A. Fernandes	
<i>Rhus pentheri</i> Zahlbr.	461

CELASTRACEAE

<i>Maytenus heterophylla</i> (Eckl. & Zeyh.) N. Robson	478 R
<i>Maytenus senegalensis</i> (Lamb.) Exell	C
Some plants in Closed Woodland areas of the Reserve correspond with <i>M. cymosus</i> forma DE 1253 described by Edwards (1967).	
<i>Maytenus undata</i> (Thunb.) Blakelock	C
<i>Cassine aethiopica</i> Thunb.	474
<i>Cassine papillosa</i> (Hochst.) Kuntze	O
<i>Cassine transvaalensis</i> (Burtt Davy) Codd	457 O

ICACINACEAE

Pyrenacantha grandiflora Baill.

SAPINDACEAE

Deinbollia oblongifolia (E. Mey.) Radlk.
Pappea capensis Eckl. & Zeyh.
Hippobromus pauciflorus (L.f.) Radlk.

RHAMNACEAE

Zizyphus mucronata Willd.
Berchemia zeyheri (Sond.) Grubov

HETEROPYXIDACEAE

Heteropyxis natalensis Harv.

VITACEAE

<i>Rhoicissus digitata</i> (L.f.) Gilg & Brandt	
<i>Rhoicissus tomentosa</i> (Lam.) Wild & Drummond	593
<i>Cissus quadrangularis</i> L.	
<i>Cissus rotundifolia</i> (Forsk.) Vahl	624
<i>Cyphostemma schlechteri</i> (Gilg & Brandt) Desc. ex Wild & Drummond	623

TILIACEAE

<i>Grewia bicolor</i> Juss.	473
<i>Grewia caffra</i> Meisn.	608
<i>Grewia flava</i> DC.	
<i>Grewia flavescens</i> Juss.	
<i>Grewia hexamita</i> Burret	
<i>Grewia monticola</i> Sond.	639
<i>Grewia occidentalis</i> L.	609
<i>Grewia</i> sp. cf. <i>kwebensis</i> N.E. Br.	
<i>Grewia subspathulata</i> N.E. Br.	
<i>Grewia villosa</i> Willd.	494

MALVACEAE

<i>Abutilon austro-africanum</i> Hochr.	
<i>Abutilon</i> sp.	535
<i>Hibiscus pusillus</i> Thunb.	632
<i>Thespesia acutiloba</i> (Bak.f.) Exell & Mendonca	456
<i>Cienfuegosia hildebrandtii</i> Garcke	631
<i>Gossypium herbaceum</i> L. var. <i>africanum</i> (Watt) Hutch. & Ghose	546

STERCULIACEAE

<i>Melhania polygama</i> Verdoorn	
<i>Melhania didyma</i> Eckl. & Zeyh.	
<i>Dombeya cymosa</i> Harv.	475
<i>Dombeya rotundifolia</i> (Hochst.) Planch.	
<i>Waltheria indica</i> L.	

OCHNACEAE

<i>Ochna natalitia</i> (Meisn.) Walp	545
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CLUSIACEAE

<i>Garcinia livingstonei</i> T. Anders.	503
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FLACOURTIACEAE

<i>Scolopia zeyheri</i> (Nees) Szyszyl.	
<i>Dovyalis caffra</i> (Hook.f. & Harv.) Hook.f.	

CACTACEAE

<i>Rhipsalis baccifera</i> (J. Mill.) Stearn	
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THYMELAEACEAE

<i>Lasiosiphon splendens</i> Endl.	622
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LYTHRACEAE

<i>Ammannia</i> sp.	
<i>Galpinia transvaalica</i> N.E. Br.	

COMBRETACEAE

<i>Combretum apiculatum</i> Sond.	486	O
<i>Combretum erythrophyllum</i> (Burch.) Sond.	484	O
<i>Combretum molle</i> R. Br. ex G. Don		O
<i>Terminalia phanerophlebia</i> Engl. & Diels	485	O

MYRTACEAE

<i>Syzygium guineense</i> (Willd.) DC.		R
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ONAGRACEAE

<i>Oenothera rosea</i> L'Hérit. ex Ait.		
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ARALIACEAE

<i>Cussonia zuluensis</i> Strey ined.	594	
<i>Cussonia spicata</i> Thunb.		

PRIMULACEAE

<i>Samolus valerandi</i> L.		
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PLUMBAGINACEAE

<i>Plumbago auriculata</i> Lam.		
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SAPOTACEAE

<i>Sideroxylon inerme</i> L.	472	C
<i>Mimusops obovata</i> Sond.	588	C
<i>Manilkara concolor</i> (Harv. ex C.H. Wr.) Gerstner		

EBENACEAE

<i>Euclea crispa</i> (Thunb.) Guerke var. <i>crispa</i>		
<i>Euclea divinorum</i> Hiern		C
<i>Euclea natalensis</i> A. DC.		C
<i>Euclea schimperi</i> (A. DC.) Dandy var. <i>daphnoides</i> (Hiern) De Winter		C
<i>Euclea undulata</i> Thunb. var. <i>undulata</i>	489	C
<i>Diospyros dichrophylla</i> (Gand.) De Winter	459	
<i>Diospyros glandulifera</i> De Winter	462	
<i>Diospyros lycioides</i> Desf. ssp. <i>sericea</i> (Bernh.) De Winter		
<i>Diospyros simii</i> (Knutze) De Winter		

OLEACEAE

<i>Olea africana</i> Mill.	493	C
<i>Jasminum multipartitum</i> Hochst.	590	

SALVADORACEAE

<i>Azima tetracantha</i> Lam.	554	R
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LOGANIACEAE

Strychnos madagascariensis Poir.*Strychnos spinosa* Lam.*Nuxia oppositifolia* (Hochst.) Benth.O
O
497

GENTIANACEAE

Chironia krebsii Griseb.

APOCYNACEAE

Rauvolfia caffra Sond.*Strophanthus gerrardii* Stapf*Wrightia natalensis* Stapf501 R
650

PERIPLOCACEAE

Stomatostemma monteiroae (Oliv.) N.E. Br.*Stomatostemma* sp.*Raphionacme elata* N.E. Br.

ASCLEPIADACEAE

Xysmalobium sp.*Ceropegia* sp.*Emplectanthus cordatus* N.E. Br.*Fockea tugelensis* N.E. Br.

CONVOLVULACEAE

Ipomoea plebeia R. Br. ssp. *africana* A. Meeuse

BORAGINACEAE

Cordia ovalis R. Br.*Ehretia rigida* (Thunb.) Druce*Heliotropium ciliatum* Kaplan*Heliotropium steudneri* Vatke*Heliotropium strigosum* Willd.*Trichodesma angustifolium* Bak.

483

531

VERBENACEAE

Chascanum hederaceum (Sond.) Moldenke var. *natalense* (H.H.W. Pearson)
Moldenke*Chascanum schlechteri* (Guerke) Moldenke

612

LABIATAE

Leucas glabrata (Vahl) R. Br. ex Benth.*Hyptis pectinata* (L.) Poir.*Coleus* sp.*Becium* sp.*Orthosiphon suffrutescens* (Thonning) J.K. Morton

555

532

SOLANACEAE

Lycium acutifolium E. Mey.

Lycium sp.

Solanum coccineum Jacq.

Solanum panduraeforme E. Mey.

607

SCROPHULARIACEAE

Veronica anagallis-aquatica Bernh.

Striga bilabiata (Thunb.) Kuntze ssp. *bilabiata*

Striga gesnerioides (Willd.) Vatke ex Engl.

SELAGINACEAE

Selago racemosa Bernh.

BIGNONIACEAE

Tecomaria capensis (Thunb.) Spach.

Kigelia africana (Lam.) Benth.

455

R

PEDALIACEAE

Ceratotheca triloba (Bernh.) Hook.f.

ACANTHACEAE

Thunbergia atriplicifolia E. Mey.

Thunbergia dregeana Nees

Chaetacanthus burchellii Nees

Ruellia patula Jacq.

Lepidagathis scabra C.B. Cl.

Barleria elegans S. Moore

Barleria obtusa Nees

Blepharis integrifolia (L.f.) E. Mey. ex Schinz

Crossandra fruticulosa Lindau

Crossandra greenstockii S. Moore

Asystasia sp.

Dicliptera clinopodia Nees

Ecbolium amplexicaule S. Moore

Justicia flava (Vahl) Vahl

Justicia petiolaris E. Mey. ex C.B. Cl.

598

606

636

530

635

527a

634

633

528

RUBIACEAE

Kohautia sp. probably *K. caespitosa* Schnizlein

Kohautia virgata (Willd.) Brem.

Xeromphis obovata (Hochst.) Keay

Xeromphis rudis (E. Mey. ex Harv.) Codd

Gardenia spatulifolia Stapf & Hutch.

Canthium setiflorum Hiern

Canthium spinosum (Klotzsch) Kuntze

Plectroniella armata (K.Schum.) Robyns

C

O

625

516

621

454 C

Dinocanthium hystrix Brem.

Pavetta delagoensis Brem.

Pavetta graciliflora Brem.

CURCUBITACEAE

Cucumis metuliferus E. Mey. ex Naud.

CAMPANULACEAE

Lobelia filiformis Lam. var. *natalensis* (A. DC.) E. Wimm.

COMPOSITAE

Vernonia capensis (Houtt.) Druce 630

Vernonia fastigiata Oliv. & Hiern

Ageratum conyzoides L.

Felicia lutea N.E. Br. 637

Felicia muricata (Thunb.) Nees 638

Nidorella resedifolia DC. 602

Brachylaena ilicifolia (Lam.) Phill. & Schweick.

Tarchonanthus camphoratus L.

Tarchonanthus galpinii Hutch. & Phill. 502

Tarchonanthus trilobus DC. var. *galpinii* (Hutch. & Phill.) J. Parva

Blumea cafra (DC.) O. Hoffm.

Pluchea dioscoridis (L.) DC. 453

Sphaeranthus peduncularis DC.

Gnaphalium luteo-album L.

Helichrysum leptolepis DC.

Helichrysum nudifolium (L.) Less. var. *leiopodium* (DC.) Moeser

Helichrysum rugulosum Less. 611

Helichrysum undatum (Thunb.) Less. 412

Pulicaria scabra (Thunb.) Druce

Zinnia peruviana (L.) L.

Flaveria bidentis (L.) Kuntze 570

Schkuhria pinnata (Lam.) Cabrera 559

Cotula anthemoides L.

Senecio bupleuroides DC.

Senecio madagascariensis Poir.

Senecio sp. aff. *barbertonicus* Klatt

Senecio viminalis Brem.

Berkheya erysithales (DC.) Roessler

SUGAR COMPOSITION, TOTAL NITROGEN AND ACCUMULATION OF C-¹⁴ ASSIMILATES IN FLORAL NECTARIES OF *PROTEA* SPECIES

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ABSTRACT

Sugar composition of nectar of six species of *Protea* was analysed by gas-liquid chromatography and consisted of sucrose, fructose and glucose in varying proportions. Total nitrogen content of nectar of *P. repens* and *P. neriifolia* was very low. Evidence is presented that nectar produced by inflorescences (e.g. *P. repens* and *P. neriifolia*) which are bird-pollinated are dominated by fructose and glucose whereas nectar of putatively rodent-pollinated inflorescences (e.g. *P. tenax*, *P. humiflora* and *P. denticulata*) contain mixtures of sucrose, fructose and glucose. By exposing leaves of flowering shoots of *P. neriifolia* to ¹⁴CO₂, studies revealed that bracts accumulate C-¹⁴ assimilates and translocation of compounds from the leaves to the floral nectaries was not affected by night and day incubation periods.

UITTREKSEL

DIE SUIKER SAMESTELLING, TOTALE STIKSTOF EN 'N OPEENHOPIG VAN C-¹⁴ ASSIMILATE IN DIE BLOMNEKTARKLIERE VAN *PROTEA* SOORTE

Die suiker samestelling van nektar van ses *Protea* soorte is met gasvloeistof-kromatografie analiseer en dit het bestaan uit sukrose, fruktose en glukose in wisselende verhoudings. Die totale stikstof inhoud van die nektar van *P. repens* en *P. neriifolia* was baie laag. Bewys word gelever dat die nektar wat deur bloeiwyses (bv. *P. repens* en *P. neriifolia*) wat deur voëls bestuif word, meer fruktose en glukose bevat, terwyl die nektar van die bloeiwyses van gewaande knaagdier bestuifde soorte (bv. *P. tenax*, *P. humiflora* en *P. denticulata*) mengsels van sukrose, fruktose en glukose bevat. Deur blare van blom-mende lote van *P. neriifolia* aan ¹⁴CO₂ bloot te stel, het dit geblyk dat die skutblare die C-¹⁴ ophoop en dat die beweging van verbindings van die blare na die blomnektarkliere nie beïnvloed was deur die dag en nag broeiperiodes nie.

INTRODUCTION

The genus *Protea* forms a conspicuous element of the fynbos vegetation of the south-western Cape (Taylor, 1978). Many *Protea* species require cross-pollination (Horn, 1962) and some are classified as either bird-pollinating or rodent-pollinating species (Rourke and Wiens, 1977), although other pollination systems probably occur in the genus. The potential pollinators are attracted to the inflorescences where nectar may be produced in millilitre quantities. The flowers of *Embothrium lanceolatum* and *Grevillea robusta*, South American and Australian genera respectively of the Proteaceae, produce nectar which is largely composed of sucrose and the pollinators of these species are unknown (Per-

cival, 1961). Very little attention has been given to the quality and quantity of nectar produced by different species of *Protea*. This paper describes the production, carbohydrate composition and total nitrogen of floral nectar of a number of *Protea* species indigenous to the south-western Cape.

The mechanisms of nectar production are not fully understood although models have been suggested (Reed, Findlay and Mercer, 1971; Lüttge and Schnepf, 1976). As a first step in the understanding of *Protea* nectar physiology, the translocation of C-¹⁴ assimilates from fed leaves to nectar glands and bracts of inflorescences of *P. neriifolia* was undertaken.

MATERIAL AND METHODS

All the inflorescences were selected from *Protea* shrubs growing on the same aspect and under similar soil conditions at the National Botanic Gardens, Kirstenbosch, Cape Town. Only one population of a given species was sampled at 12h00–15h00 on sunny days at least 3 days after rains during April–August, 1978. The inflorescences were grouped into three age categories: new, half-new and old inflorescences.

1. New—a stage when the mature bracts are open revealing erect, densely packed and unopened florets.
2. Half-new—a stage when the florets are beginning to open in which the erect style becomes fully exposed functioning as the pollen presenter.
3. Old—a stage when all the florets in the inflorescences are completely open.

Nectar was removed from the inflorescences by means of a Pasteur pipette and samples were transferred to the laboratory and immediately frozen. The carbohydrate composition was identified and quantitatively determined by means of gas-liquid chromatography of their trimethylsilyl (TMS) derivatives using the methods of Holligan and Drew (1971), and Mitchell and Roberts (1973). Each sample for analysis contained 50 $\mu\ell$ nectar and 1 mg erythritol as the internal standard. Carbohydrates were characterised by comparison of their retention times relative to erythritol with those of standard compounds. TMS derivatives of standard carbohydrates were co-chromatographed to confirm the identity of individual peaks. A quantitative estimate was made by measuring the peak heights and referring to calibration curves of standard carbohydrates.

For total nitrogen determinations, 4 ml of three nectar samples of each species was analysed by means of the micro-Kjeldahl method.

Nectar volume in each inflorescence was estimated by initially collecting nectar using a Pasteur pipette and any residual nectar was removed by rinsing with 100 ml of distilled water. Any contamination of the diluted nectar by pollen and other solids during the rinsing process was kept to a minimum. Aliquots of pure nectar (0.5–0.2 ml) and diluted nectar (3.5 ml) were oven-dried at 80°C and

weighed. The total nectar volume in each inflorescence was then determined using the following formula:

$$\frac{100 \text{ (vol. pure nectar) (wt. dil. nectar)}}{\text{(vol. dil. nectar) (wt. pure nectar)}} + \frac{\text{orig. vol.}}{\text{pure nectar}}$$

C_{14} assimilation studies were undertaken by enclosing the foliose part of shoots of *P. neriifolia* containing one half-new inflorescence in a bell jar (300 × 250 mm). The base of the stem was immersed in a beaker of distilled water. The stem projecting the inflorescence through the top of the bell jar was sealed with Plasticine. An excess of 10 % lactic acid was added to 20 μ Ci of sodium C_{14} carbonate in a beaker in the bell jar to release $^{14}\text{CO}_2$. At the end of 30 minute incubation, the bell jar was removed to allow the shoots to undergo 24 hour "chase" period. For the duration of the experiment, the excised flowering shoots were maintained at 25 °C day and 20 °C night temperatures with an 8 hour day-length of 30 000 lux from fluorescent and tungsten lamps. Nectar was extracted during the day and night phases of incubation and at the end of 24 hour "chase" period the fed leaves and bracts were removed and plunged into boiling 80 % ethanol.

Aliquots of nectar (0.1 ml) were blended with 2 ml Beckman G.P. scintillation cocktail. Leaf and bract tissues were homogenised in 80 % ethanol using an Ultra-Turrax homogeniser. The ethanol-soluble extracts were filtered from the residue using Whatman no. 1 filter paper and both extracts were evaporated to dryness. The ethanol-soluble components were dissolved in distilled water and aliquots (0.1 ml) were blended with 2 ml Beckman G.P. scintillation cocktail. Portions of the insoluble components (100 mg) were transferred to scintillation vials and solubilised for 24 hours in 0.2 ml 60 % perchloric acid and 0.4 ml 30 % H_2O_2 using the method of Lobban (1974). After solubilisation, 5 ml of Packard Dimulume was added. Radioactivity was monitored on a Beckman LS 150 scintillation spectrometer for 20 minutes. All counts were converted to disintegrations per minute (DPM) after correcting for quenching using external standard ratio and C_{14} toluene.

RESULTS

Carbohydrate composition, nitrogen content and total volume of nectar

The sugar composition of the nectar consists of sucrose, glucose and fructose (Table 1). Fructose and glucose was detected in approximately equal proportions indicating that these reducing sugars are probably derived from enzymatic

TABLE 1.
Carbohydrate composition (mg ml⁻¹) of nectar of *Protea* spp.

		Fructose	Glucose	Sucrose
<i>P. repens</i> (L.) L.	New	55.5 ± 1.6	35.6 ± 0.9	—0
	Half-new	139.1 ± 28.7	110.1 ± 15.6	2.1 ± 2.1
	Old	27.7 ± 23.4	14.7 ± 11.9	2.3 ± 2.2
<i>P. nerifolia</i> (L.) L.	New	27.7 ± 13.4	21.3 ± 12.1	1.1 ± 0.7
	Half-new	44.1 ± 23.0	43.9 ± 22.1	1.6 ± 0.8
<i>P. sulphurea</i> Phill.	New	27.7 ± 8.0	61.9 ± 8.9	53.0 ± 7.3
	Half-new	62.5 ± 4.7	46.6 ± 5.2	77.3 ± 4.4
<i>P. tenax</i> (Salisb.) R.Br.	New	63.1 ± 12.8	26.1 ± 10.8	60.4 ± 35.2
	Half-new	70.0 ± 10.6	61.2 ± 9.8	40.4 ± 11.4
<i>P. denticulata</i> Rourke	New	34.9 ± 4.6	31.9 ± 4.7	66.7 ± 16.9
	Half-new	29.9 ± 5.2	26.5 ± 5.2	9.4 ± 1.7
<i>P. longifolia</i> Andr.	Half-new	46.3 ± 16.1	128.5 ± 25.8	191.6 ± 77.7
	Old	68.8 ± 8.6	80.5 ± 31.3	128.3 ± 49.9
<i>P. humiflora</i> Andr.	Half-new	46.3 ± 4.6	31.9 ± 4.7	66.7 ± 16.9

Values are means of three separate analyses ± standard error of the mean.

hydrolysis of sucrose (Von Handel, Haeger and Hansen, 1972). There appears to be considerable interspecific variation of nectar composition. The sugar composition ranges from almost exclusively fructose-glucose (*P. repens* and *P. neriifolia*) to a balanced mixture of sucrose, glucose and fructose (*P. sulphurea*, *P. tenax*, *P. humiflora* and *P. denticulata*) to a sucrose dominating nectar (*P. longifolia*).

Only sufficient nectar was collected from *P. repens* and *P. neriifolia* for total nitrogen determinations. Total nitrogen content of *P. neriifolia* and *P. repens* was $46,7 \pm 11,7$ and $36,5 \pm 7,4 \mu\text{g ml}^{-1}$ respectively.

Total volume of nectar in the inflorescences is shown in Table 2 and *P. neriifolia* and *P. repens* produced the largest volume of nectar.

TABLE 2.
Volume of nectar (ml inflorescence⁻¹) produced in the inflorescences of *Protea* spp.

	New	Half-new	Old
<i>P. repens</i>	4,4 ± 0,6	4,9 ± 0,4	0,6 ± 0,2
<i>P. neriifolia</i>	5,2 ± 0,0	5,3 ± 0,0	6,5 ± 0,2
<i>P. sulphurea</i>	0,1 ± 0,1	1,3 ± 0,1	—
<i>P. denticulata</i>	—	0,6 ± 0,5	—
<i>P. tenax</i>	0,2 ± 0,1	0,4 ± 0,2	—
<i>P. longifolia</i>	—	0,9 ± 0,1	0,3 ± 0,0

Results are means of three separate determinations ± standard error of the mean.
(—) denotes no analysis.

Translocation of C₁₄ labelled assimilates to inflorescences of *P. neriifolia*

Figure 1 shows the radioactivity of nectar collected at intervals of time after exposure of fed leaves to ¹⁴CO₂. There was a 2 hour lag period and then radioactivity in the nectar increased to a maximum after 20 hours during the "chase" period. The accumulation of activity was not affected by the dark phase of incubation.

At the end of the 24 hour "chase" period, the fed leaves and bracts of the inflorescences were analysed for ethanol-soluble and -insoluble radioactive compounds. A significant proportion of C₁₄ labelled assimilates was translocated to the bracts and these assimilates were stored as insoluble compounds (Table 3).

DISCUSSION

Nectar of *Protea* species consists entirely of sucrose, glucose and fructose with nitrogenous compounds forming a minor component. C₁₄ assimilation studies of *P. neriifolia* have revealed that translocation of compounds to floral nectaries is

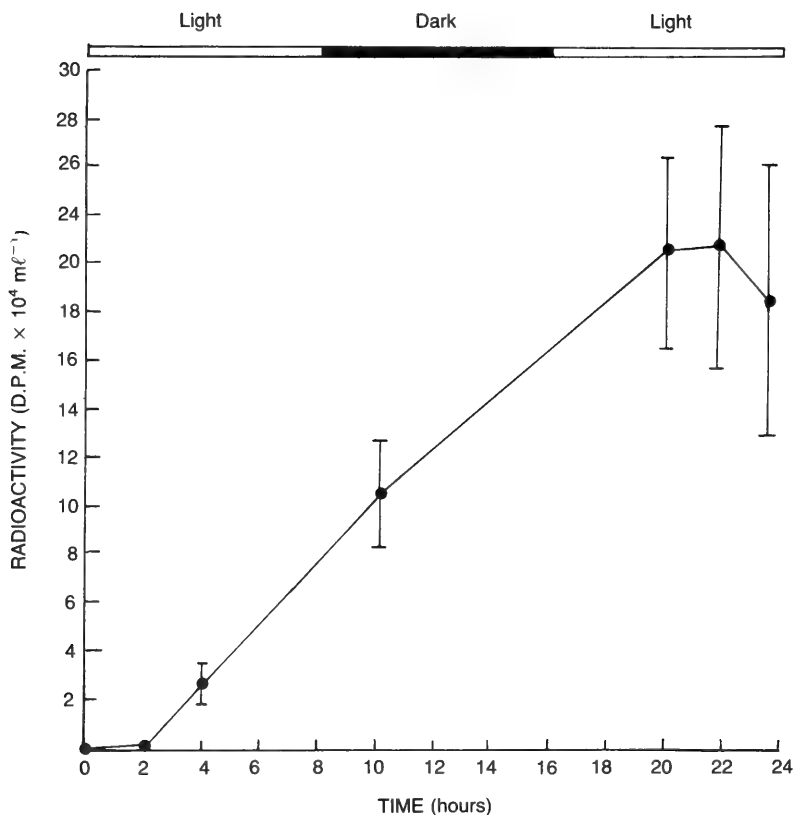


FIG. 1.

Radioactivity of nectar from inflorescences of *P. neriifolia* during the "chase" period after feeding leaves of shoots in $^{14}\text{CO}_2$ for 30 minutes.

not affected by dark incubation. The accumulated assimilates in the bracts may act as an alternative source of carbon which could then be re-directed to the floral nectaries.

There was however, a wide range of nectar types among *Protea* species in terms of the proportions of sucrose, fructose and glucose. The intraspecific constancy of sugar composition in *Protea* nectars is in agreement with other data (Wykes, 1952a; Percival, 1961; Van Handel *et al.*, 1972; Rowley, 1976). The

TABLE 3.

Recovered radioactivity in the fed leaves, bracts and floral nectar of *P. neriifolia* 24 hours after exposure to $^{14}CO_2$.

	Fed leaves	Bracts	Nectar
Total DPM $\times 10^4$	185,2 \pm 42,3	21,5 \pm 6,2	78,5 \pm 6,4
Ethanol-soluble (%)	0,9	0,7	100
Ethanol-insoluble (%)	99,1	99,3	0

Results expressed as means of three separate feeding experiments \pm standard error of the mean.

The shoots contained one half-new inflorescence and three leaves with a mean area of $75,0 \pm 9,6$ cm² leaf⁻¹.

results presented in this paper agree with those of Mostert *et al.*, (1980) who found that *P. repens* nectar consisted of reducing sugars, although G.L.C. analysis showed negligible amounts of sucrose compared with small but significant levels of this disaccharide in these studies.

Mostert *et al.* (1980) demonstrated that nectar of *P. repens* could be a major energy source for the Cape sugarbird. *P. repens* nectar was however low in protein and amino acids, but insects in the inflorescences may be the major source of nitrogen for the Cape sugarbird. In this study, *P. repens* and *P. neriifolia* produced the largest volume of nectar. Both of these species have large, brightly coloured terminal inflorescences, which are important features for bird pollination. The large, conspicuous and erect inflorescences of *P. longifolia* have green-coloured bracts and produce small quantities of sucrose-dominated nectar. The question arises whether the pollination strategy of *P. longifolia* is very different from that of related species.

The rodent-pollinated species appear to have small saucer-shaped dull coloured inflorescences and are borne at or near the ground (Rourke and Wiens, 1977). In this study, species which may be rodent-pollinated (e.g. *P. tenax* and *P. denticulata*) produce small volumes of nectar rich in sucrose. Bracts of *P. amplexicaulis* are known to be eaten by the rodent pollinators and thus may act as an alternative food source (Rourke, pers. comm.).

Direct evidence of pollinators preferring specific components in the nectar is very limited. Attraction by honeybees can be determined by the composition and concentration of nectar (Butler, 1945; Wykes, 1952b). A hierarchy of factors influencing taste and colour preferences has been demonstrated in hummingbirds (Stiles, 1976). Hummingbirds preferred solutions containing sucrose (Stiles, 1976), whereas starlings are attracted to glucose and fructose solutions but rejected sucrose (Schüler, 1978).

Preliminary "T" maze experiments using rodents indicate that test animals forage on *P. humiflora* almost exclusively when presented with a choice of it and *P. repens* (Wiens, pers. comm.). Until more information on pollination activity

in *Protea* is available, discussion on the possible links between nectar characteristics and pollination ecology remains largely speculative.

ACKNOWLEDGEMENTS

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 22-24

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22. *ERIOSPERMUM BOWIEANUM* Bak.

CHROMOSOME NUMBER: $2n = 14$ (Figs 1a, b).

ORIGIN OF MATERIAL: Robertson, C.P. (Collection *P. L. Perry* 273). Compton Herbarium accession no. 119553 (NBG).

METHOD OF PREPARATION: Root tip material. Colchicine pretreatment, feulgen/ acetic orcein staining.

OBSERVATIONS: In the plant examined, the smallest chromosome showed pronounced heteromorphism, the one chromosome being larger and more metacentric than the other (Fig. 1a).

23. *ERIOSPERMUM PARADOXUM* Ker Gawl. (= *E. cylindricum* Marl.)

CHROMOSOME NUMBER: $2n = 14$ (Figs 2a, b).

ORIGIN OF MATERIAL: De Doorns, C.P. (Collection *M. B. Bayer* 886). Compton Herbarium accession no. 119561 (NBG).

METHOD OF PREPARATION: As in 22.

24. *ERIOSPERMUM MULTIFIDUM* Marl.

CHROMOSOME NUMBER: $2n = 14$ (Figs 3a, b).

ORIGIN OF MATERIAL: Springbok, C.P. (Collection *P. V. Bruyns* 1466). Compton Herbarium accession no. 121557 (NBG).

METHOD OF PREPARATION: As in 22.

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FIG. 1A.

E. bowieanum, somatic metaphase. Bar represents 10 μ . Larger arrows indicate secondary constrictions, smaller arrows the heteromorphic smallest chromosome pair.

1b

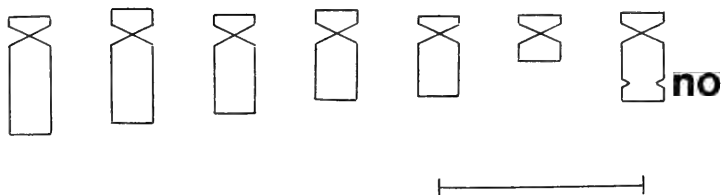


FIG. 1B.

E. bowieanum, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

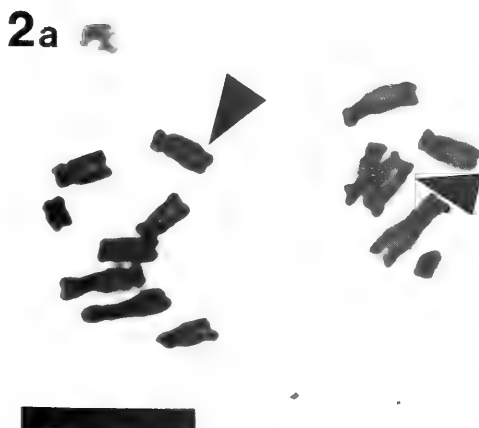


FIG. 2A.

E. paradoxum, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

2b

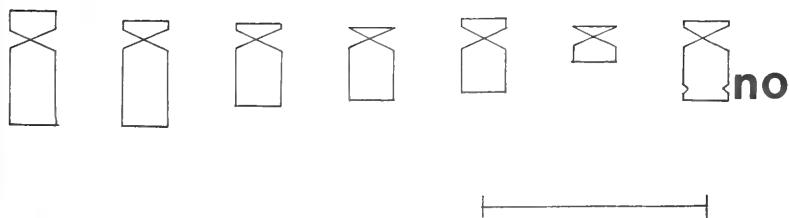


FIG. 2B.

E. paradoxum, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

3a



FIG. 3A.

E. multifidum, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

3b

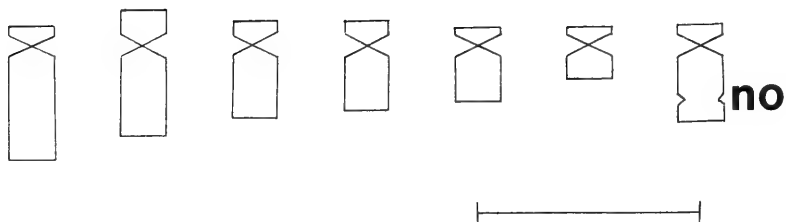


FIG. 3B.

E. multifidum, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.

STUDIES IN THE GENERA OF THE DIOSMEAE (RUTACEAE): 12. A REVISION OF THE GENUS *PHYLLOSMA* AND A PROPOSED NEW GENUS *SHEILANTHERA*

ION WILLIAMS

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ABSTRACT

The diagnostic characters of the monotypic genus *Phyllosma* are redefined to include one more species transferred from the genus *Acmadenia*. A monotypic genus is proposed to accommodate the new species *Sheilanthra pubens* Williams.

UITTREKSEL

STUDIES IN DIE GENERA VAN DIE *DIOSMEAE* (RUTACEAE): 12. 'N HERSIENING VAN DIE GESLAG *PHYLLOSMA* EN 'N VOORGESTELDE NUWE GESLAG *SHEILANTHERA*

Die diagnostiese kenmerke van die monotipiese geslag *Phyllosma* word herbepaal om 'n verdere soort in te sluit wat uit die geslag *Acmadenia* oorgeplaas is. 'n Monotipiese geslag word voorgestel om die nuwe soort *Sheilanthra pubens* Williams te beskryf.

HISTORICAL BACKGROUND

The monotypic genus *Phyllosma* was described by H. Bolus in 1898 from a specimen collected by Rudolph Schlechter on the Koudeberg near Wupperthal in 1896. Since then it has been collected several times, from localities widely scattered in the drier parts of the mountains of the Clanwilliam and Ceres Divisions. Bolus did not mention any herbarium in which the type material was preserved.

However the specimen (*Schlechter 8781*) in the Bolus Herbarium at the University of Cape Town is accompanied by manuscript notes in Bolus's handwriting together with his dissections of the flower. This is therefore most certainly the holotype being the material used by Bolus in the preparation of his descriptions of *Phyllosma capensis*.

***Phyllosma* H. Bolus in Engl. Bot. Jahrb. 24: 547 (1898).**

Generic type: *Phyllosma capensis* H. Bol.: CAPE—3219 (Wupperthal): Koudeberg near Wupperthal, Clanwilliam Division, (-AC), 1 200 m alt., 30/8/1886, *Schlechter 8781* (BOL).

DIAGNOSTIC CHARACTERS

The genus *Phyllosma* is distinguished by having: 1. flowers terminal, 2. petals clawed, 3. the disc closing over the ovary at first, 4. staminodes absent, 5. the stigma simple, 6. the style and filaments lengthening greatly and 7. the ovary 5-carpellate.

1. ***Phyllosma capensis*** H. Bolus in Engl. Bot. Jahrb. **24**: 457 (1898). Type: CAPE—3219 (Wupperthal): Koudeberg near Wupperthal, Clanwilliam Division (—AC), 1 300 m (4 000 ft.), alt., 30/8/1896, *Schlechter 8781* (BOL, holotype; SAM, isotype).

The following description done from fresh material amplifies that previously given by H. Bolus.

Shrubs 0,3–0,4 mm tall, growing from crevices in massive rocks of the Table Mountain Sandstone with several stems arising from a single stem at base. *Branches* short, not very numerous, variously bent; bark rough ashy-grey. *Branchlets* very short, erect, puberulous, not hidden by the leaves. *Leaves* 10–13 mm long, 2,3 mm broad, linear-oblong, thick, alternate, spreading or on new twigs ascending incurved-imbricate; apex mucronate, sub-acute; margins revolute, gland-dotted, densely pubescent at the edge, rounded at the base to a petiole 1,5 mm long, puberulous; adaxial surface at first thinly crisped puberulous becoming sub-scabrid; abaxial surface mostly enfolded with only the midrib showing, very densely short-pubescent; midrib thick, gland-dotted. *Inflorescence* terminal, 3–4 nate, sessile; petals white to pink, spreading about 15 mm diam. *Bract* 5–6,5 mm long, 2,1–1,4 mm broad, lanceolate-caudate, acute, densely puberulous on all sides; margins densely lanate-ciliate, not translucent; midrib prominent, gland-dotted. *Bracteoles* two, 5 mm long, 2 mm broad, lanceolate, acute, sub-apiculate, densely ciliate, puberulous on all sides, reddened above semi-translucent. *Calyx lobes* five, 7–7,5 mm long, 2,2–2,8 mm broad, lanceolate, acute; apex red-mucronate, pubescent; margins densely crisped ciliate; adaxial surface sparsely crisped puberulous above; abaxial surface densely puberulous; midrib prominent, gland-dotted, reddened. *Petals* five, 15 mm long overall; limb 10 mm long, 4,5 mm broad, elliptic, minutely apiculate, 3 or 4 minute hairs at the apex, pinkish-white, narrowed below to a claw 5 mm long, very sparsely pubescent at the throat on all sides but mainly up the midrib. *Staminodes* virtually absent, on the disc between the filaments one can see five minute lumps which are undoubtedly the vestiges of staminodes. *Filaments* five, becoming 11 mm long, hispid. *Anthers* five, before anthesis, 2,5 mm long, 1 mm broad, red at first becoming greenish; apical gland, 0,3 mm diam., sessile. *Pollen* 53 μ long, 22 μ broad, oblong, green. *Disc* flat, level with the base of the filaments, thin with rather irregular membranous flaps pointing inwards towards the style, at first hiding the ovary, green, nectariferous. *Stigma* 0,2 mm diam., sim-

ple, reddened. *Style* becoming 14 mm long, hispid in the lower three quarters. *Ovary* 5-carpellate, 1,2 mm long, 1,3 mm diam.; apices obtuse, densely velvety. *Fruit* 5-carpellate, 6,5 mm long, 5 mm diam., puberulous, gland-dotted and with scattered stalked glands; *horns* 4,2–4,8 mm long, erect, finger-like, obtuse, puberulous, gland-dotted and with scattered stalked glands. *Seed* 4,75 mm long, 1,75 mm broad, black, shining; aril black.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): Pakhuis, rocks, Clanwilliam Division (–AA), 21/9/1942, *Esterhuysen* 8027 (BOL, NBG); N. Cedarbergen, in rock crevices along the path from Pakhuis to Heuningvlei, 19/10/1945, *Esterhuysen* 12055 (BOL); Beacon 79, 3 800 ft., 25/9/1969, *Esterhuysen* 32227 (BOL); in montibus circa Pakhuis inter Clanwilliam et Biedouw, c.2 800 ft., –/10/1897, *MacOwan* 3259 (SAM); Bothasberg, Pakhuis Pass, –/9/1936, *Thorne s.n.* (SAM 52690); Koudeberg near Wupperthal, Clanwilliam Division (–AC), 4 000 ft., 30/8/1896, *Schlechter* 8781 (BOL, SAM); in montibus Cedarbergen prope Wupperthal, c. 4 500 ft., 4/10/1897, *Bodkin s.n.* (BOL 8954); Elandskloof, Clanwilliam/Ceres Division (–CA), 26/9/1936, *Lewis s.n.* (BOL 22049), 9/12/1940, *Esterhuysen* 3994 (BOL), 3/10/1940, *Esterhuysen* 3140 (BOL), 4 000 ft., 25/9/1936, *Compton* 6515 (NBG), 3/10/1940, *Bond* 632 (NBG), 30/9/1944, *Compton* 16158 (NBG), 24/9/1974, *Goldblatt* 2753 (NBG); Wabooms River, Ceres Division, 3 500 ft., 25/9/1936, *Compton* 6514 (NBG); Cedarberg, Sugar Loaf near Krom River, Clanwilliam Division, 8/10/1961, *Jackson s.n.* (NBG); Krom River, Clanwilliam Division (–CB), 2 500 ft., 27/9/1934, *Leighton s.n.* (BOL 21583); Ridge S. of Krom River, S. Cedarberg, 3 600 ft., 18/9/1975, *Williams* 2082 (NBG), 4/10/1953, *Esterhuysen* 20483 (BOL, NBG); Gideonkop, S. Cedarberg, Ceres Division, 3 500–4 000 ft., 6/4/1947, *Esterhuysen* 13879 (BOL), –/11/1939, *Stokoe s.n.* (SAM 30636); rocky ridge on farm Suurvlaakte E. of Bokkeveld Sneeuwkop above Winkelhaaks River, Ceres Division (–CD), 20/4/1946, *Esterhuysen* 12701 (BOL), 14/9/1975, *Esterhuysen* 33944 (BOL); Bokkeveld Sneeuwkop, 4 500 ft., 13/9/1975, *Esterhuysen* 33934 (BOL); Kleinveld on track to Bloukop, E. Cold Bokkeveld, 3 500 ft., 24/10/1975, *Williams* 2125 (NBG).

DISTRIBUTION, VARIATION AND BIOLOGY

Phyllosma capensis is found growing from crevices in massive T.M.S. rocks at altitudes of from 760 to 1 370 m (2 500–4 500 ft.) in rather dry situations in the mountains of the Clanwilliam and Ceres Divisions. No significant variation has been observed. The sticky pollen, simple stigma and presence of nectar suggests that this species is pollinated by insects.

The absence of staminodes, the very long hispid style and filaments and the leaves with revolute margins readily distinguish this species.

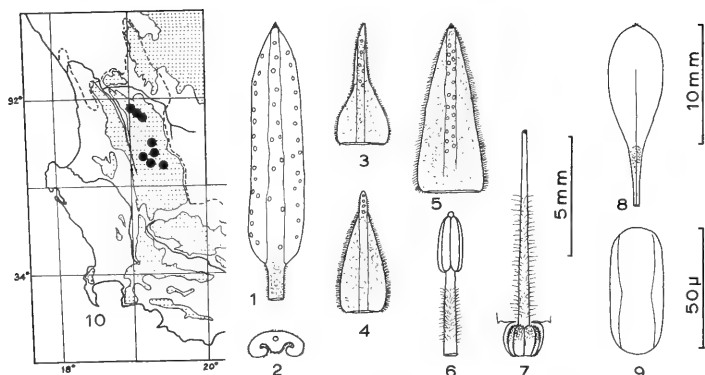


FIG. 1.

Phyllosma capensis: 1, leaf. 2, cross-section of leaf. 3, bract. 4, bracteole. 5, calyx lobe. 6, anther. 7, gynoeceum and disc. 8, petal. 9, pollen. 10, distribution.

2. *Phyllosma barosmoides* (Dümm.) Williams, comb. nov.

Acmadenia barosmoides Dummer in Journ. Bot. 51: 221 (1913):—Basionym.
Type: Alpine stony places, Langkloof, *Niven No. 11* (BM, holotype).

Shrubs 0,3 m tall, 0,6–0,9 m across, low, woody, growing from crevices in massive T.M.S. rocks. *Branches* short, glabrous, rough with leaf scars. *Branchlets* short, sparsely pubescent, hidden by the leaves. *Leaves* 6–8 mm long (including the petiole 1 mm long), 2,9–3,8 mm broad, obovate, obtuse, flat, glabrous, crowded, spreading-erect, alternate; apex with a large discoid gland often with another somewhat smaller to either side; margins thick with many gland dots, villous-ciliate at first; adaxial surface smooth, shining; abaxial surface with scattered gland dots, faintly nerved. *Inflorescence* twin, terminal, pink; *pedicel* less than 1 mm long, puberulous. *Bract* 5–6,2 mm long (including the petiole 1 mm long), 2,5 mm broad, leaf-like. *Bracteoles* two, 3,4 mm long, 0,7 mm broad, linear; apex with a flat discoid gland; margins ciliate with a few gland dots to either side above. *Calyx lobes* five, 4,8 mm long, 1,4–1,8 mm broad, oblong, glabrous, ciliate, gland-dotted near the margins above; apex with a flat discoid gland. *Petals* five, 8,5–9 mm long overall, 3,5 mm broad, elliptic, narrowing gradually to 0,5 mm at the base, glabrous; apex with a small point with one or two small hairs to either side. *Staminodes* absent. *Filaments* five, becoming 8 mm long, glabrous, filiform. *Anthers* c. 1 mm long; apical gland absolutely minute, immersed in the cleft between the thecae at the apex. *Pollen* 35 μ long, 23 μ diam., ellipsoid. *Disc* at first closes over the ovary, touches the base of the



FIG. 2.

Phyllosma capensis: Flower with part removed to show the filaments and style.

style, the very slightly larger lobes of the disc are opposite the petals. *Stigma* 0,2 mm diam., simple. *Style* becoming 10 mm long, glabrous. *Ovary* 5-carpellate, 0,8 mm long, 1 mm diam., glabrous; apices globose, inclined inwards. *Fruit* and *seed* not seen.

It appears that up to now the only person to make collections of this species with properly authenticated localities is Miss Elsie Esterhuysen of the Bolus Herbarium at the University of Cape Town. These collections have all come from high rocky places in the Waaihoek Mountains and on the Matroosberg in the South Western Cape. The locality "Langkloof" referred to by Niven therefore cannot refer to the area in Uniondale district known by that name, as stated

by Dümmer (1913). The above description, based upon dried material collected by Miss E. Esterhuysen (28899), amplifies that given by Dümmer.

SPECIMENS EXAMINED

CAPE—3319 (Worcester): Sybasberg, Waaihoek Mountains, sloping rock and ledges, north aspect, Worcester/Ceres Division (–AD), 5 500 ft., 12/1/1954, *Esterhuysen* 22569 (BOL, K); ridge on Waaihoek Peak leading to Tarantula Peak, Ceres Division, 6 000 ft., 15/1/1961, *Esterhuysen* 28732 (BOL); Delville Peak, Waaihoek Mountains and along ridge leading to Mitchell's Peak, Ceres Division, 16/1/1961, *Esterhuysen* 28739 (BM, BOL); Mitchell's Peak, Waaihoek Mountains, amongst rocks on ridge, Ceres Division, 5 600–5 700 ft., 16/1/1961, *Esterhuysen* 28744 (BOL); Waaihoek Peak, rocky ridge on east side of peak, overlooking Witels, Ceres Division, 25/2/1961, *Esterhuysen* 28899 (BOL); Matroosberg, S. E. slopes below "Coat of Arms", Worcester Division (–BC), 5 000 ft., 7/4/1958, *Esterhuysen* 27721 (BOL); Matroosberg, along narrow crest of rocky ridge leading to peak from east-north side, opposite Sonklip, Ceres Division, c. 5 000 ft., 2/6/1968, *Esterhuysen* 31965 (BOL).

Without precise locality: Alpine stony places, Langkloof, *Niven* 11 (BM). Probably Seven Weeks Poort Mtns. 5 800–6 000 ft., –/10/–, *Marloth* 7950 (BOL).

DISTRIBUTION

As far as is known *Phyllosma barosmoides* is to be found growing only in rock crevices on high mountain ridges of the Matroosberg, at altitudes of from 1 500 to 1 800 m (5 000–6 000 ft.).

The absence of staminodes, the very long glabrous style and filaments and the flat leaves with a discoid gland at the apex readily distinguish this plant from all others.

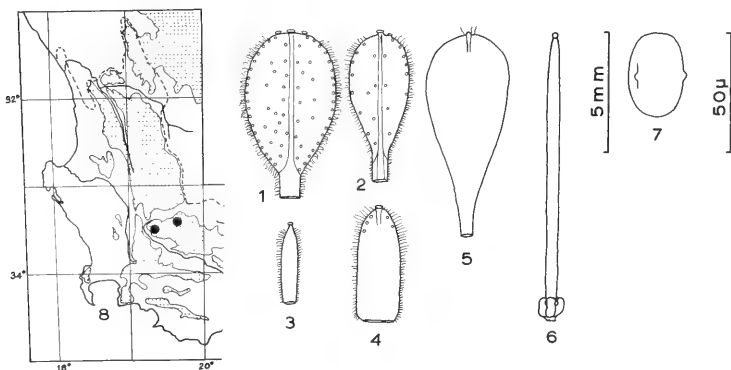


FIG. 3.

Phyllosma barosmoides: 1, leaf. 2, bract. 3, bracteole. 4, calyx lobe. 5, petal. 6, gynoecium. 7, pollen. 8, distribution.

Sheilanthera Williams, gen. nov. (Rutaceae-Diosmeae)

Petala anguste unguiculata sparsim pubescentia. *Staminodia* nulla. *Filamentia* brevia, glabra. *Stylus* brevis, glaber. *Anthera* sparsim pubescentia, glandula sessilia coronata. *Discus* obvallatus, ovarium longe excedens. *Stigma* capitellatum. *Ovarium* dense pubescens. Affinis *Phyllosma* sed ita differt petalo flabelliformi, filamentis styloque perbrevis et stigma capitata.

Sheilanthera is a distinct genus in the Rutaceae, tribe *Diosmeae*, having a flower with the petal narrowly clawed, thinly pubescent at the throat, lacking staminodes, with the filaments and style short and glabrous, with the anther thinly pubescent terminating in a sessile apical gland, with the disc obvallate exceeding the ovary by a long way, with the stigma capitellate and with the ovary densely pubescent. In particular in its fan-shaped petal, very short style and filaments and capitate stigma, it differs from the genus *Phyllosma*.

Type: *Sheilanthera pubens* Williams.

Sheilanthera pubens Williams, sp. nov. propria propter florem staminodiis carentibus, antheris sparsim pubescentibus, et ovario dense pubescenti.

Frutex 0,3–0,4 m, densus, rotundatus, expansus, ad basim monocaulis. *Rami* numerosi, breves, patentes, glabri, saepe dichotomi. *Ramuli* numerosi, breves, erectiusculi, pubescentes. *Folia* 6–9 mm longa (petiolo 1 mm longo incluso), 2–2,5 mm lata, elliptico-oblonga, obtusa, alterna, patentia; marginibus revolutis crassis glanduloso-punctatis; costa conspicua lateri-pubescenti. *Inflorescentia* 9 mm diam., terminalia 1–3 nata, primo rosea. *Bractea* 3,3 mm longa, 1,5 mm lata, lanceolata, sub-acute, villosa; marginibus villosa-ciliatis, glanduloso-stipitatis. *Bracteolae* duae, 3 mm longae, 1 mm latae, lanceolatae, acutae; marginibus crispo-ciliatis, glanduloso-stipitatis; pagina abaxiali villosa; pagina adaxiali sparsim pubescenti, 1–3 glanduloso-punctata. *Sepala* quinque, 3,3–3,5 mm longa, 1,7–2,5 mm lata, ovato-lanceolata, sub-acute; marginibus villosa-ciliatis, ad apice stipitato-glandulosis. *Calyx* pubescens, stipitato-glandulosus. *Petala* quinque 6 mm longa; *limbus* 3,5–4 mm longus, 3,8–4,5 mm latus, flabellatus, ad basim sparsim pubescens; *unguis* 2,5 mm longus, 0,7 mm latus, linearis. *Staminodia* nulla. *Filamenta* quinque, 2 mm longa, acicularia, glabra. *Antherae* quinque, ante-anthesin 1,2 mm longae, 1 mm latae, vinosae, sparsim pubescentes, glandula sessilia coronata. *Pollen* 38 μ longum, 16 μ latum, oblongum. *Discus* obvallatus, ovarium longe excedens, nectarifer. *Stigma* 5-lobatum, 0,3 mm diam., viridum, capitellatum. *Stylus* 1,5 mm longus, erectus. *Ovarium* plus-minusve 0,5 mm longum, plus-minusve 0,7 mm latum, dense pubescens. *Fructus* et *semen* incognitus.

Type: CAPE—3219 (Wupperthal): ridge S. E. of Bloukop, eastern Cold Bokkeveld, Ceres Division (—CB), 1615 m (5 300 ft.) alt., 24/10/1975, Williams 2122 (NBG, holotype; K, PRE, MO, S, BOL, STE, M, NSW).

This unique plant was discovered by Miss Elsie Esterhuysen in 1958 on Bloukop in the Cold Bokkeveld. As far as is known it is confined to this locality, and to one other nearby, and had never been collected by anyone else. A section of the stem 18 mm in diameter showed about 50 annual growth rings.

Shrubs 0,3–0,4 m tall, dense, rounded, spreading, single-stemmed at base. *Branches* numerous, short, spreading, glabrous, often dichotomous; bark brown, smooth, leaf scars not very prominent. *Branchlets* numerous, short, fairly erect, pubescent, light brown in colour. *Leaves* 6–9 mm long including the 1 mm long petiole, 2–2,5 mm broad, elliptic-oblong, obtuse, alternate, spreading; margins revolute, thick, with large immersed gland dots adjacent to small glandular tumuli; adaxial surface convex glabrous with a shallow median groove; abaxial surface densely pubescent in two grooves adjacent to the conspicuous gland-dotted midrib; new leaves are normally villous with stipitate glands having reddish resinous tips. *Inflorescence* terminal 1–3 nate, 9 mm diam.; petals pink fading to white. *Bract* 3,3 mm long, 1,5 mm broad, lanceolate; apex sub-acute with several stipitate glands; margins villous-ciliate with stipitate glands; adaxial surface villous, somewhat concave; abaxial surface densely crisped pubescent; midrib slightly gibbous towards the apex. *Bracteoles* two, 3 mm long, 1 mm broad, lanceolate; apex acute with a stipitate gland; margins crisped ciliate with stipitate glands; adaxial surface sparsely pubescent with one to three gland-dots towards the apex; abaxial surface villous. *Calyx* pubescent with scattered stipitate glands. *Calyx lobes* five, 3,3–3,5 mm long, 1,7–2,5 mm broad, ovate-lanceolate, sub-acute, pubescent; apex and upper margins with sticky stipitate glands; margins villous ciliate. *Petals* five, 6 mm long overall; *limb* 3 mm long, 3,8–4,5 mm broad, fan-shaped, thinly villous below, spreading; *claw* 3 mm long, 0,7 mm broad, linear, erect. *Staminodes* absent, there is no space between the erect claw and the narrow rim of the disc. *Filaments* five, becoming 2 mm long, erect, glabrous, acicular, reddened. *Anthers* five, 1,2 mm long, 1 mm broad, wine-coloured, rather thinly pubescent, apical gland sessile. *Pollen* 38 μ long, 16 μ broad, oblong. *Disc* obvallate, exceeding the ovary by a long way, wine-coloured, sinuate, level, exudes nectar. *Stigma* 5-lobed, 0,3 mm diam., capitellate, dark green. *Style* becoming 1,5 mm long, glabrous, erect, wine-coloured. *Ovary* 5-carpellate, \pm 0,5 mm long, \pm 0,7 mm diam., densely pubescent; each lobe with a globose apical gland. *Fruit* and *seed* not seen.

SPECIMENS EXAMINED

CAPE—3219 (Wupperthal): Blaauwkoop, Cold Bokkeveld, rocky plateau and amongst rocks, Ceres Division (–CB), 4 500–5 500 ft. alt., 1/10/1958, Esterhuysen 27889 (BOL, K, MO, S, LD, L, UC, M, C, GRA, E); ridge S.E. of Bloukop, eastern Cold Bokkeveld, Ceres Division, 1615 m (5 300 ft.) alt., 24/10/1975, Williams 2122 (NBG, K, PRE, MO, S, BOL, STE, M, NSW); Bok-

keveld Sneeuwkop, rocky koppie below the shale band on the north side, Ceres Division (-CD), 30/3/1963, *Esterhuysen s.n.* (BOL).

DISCUSSION

Sheilantha pubens is a unique species that differs from all species of: *Acmadenia* which possess staminodes, have the anther glabrous and the ovary not densely pubescent;

Adenandra which have anthers with stipitate glands;

Agathosma which have a range of staminodes from terete to petaloid;

Coleonema which have staminodes connate with the petal;

Diosma which have sessile petals and the disc spreading;

Euchaetis which have transversely bearded petals;

Macrostylis which have the style and filaments protruding a long way and the ovary usually 3-carpellate;

Phyllosma which has the style and filaments very long and the stigma minute or simple.

It possesses leaves similar to those of *Phyllosma* with rolled-in margins and has stipitate glands similar to those found in *Acmadenia bodkinii* (Schltr.) Strid, *Acmadenia rourkeana* Williams (ms.), *Acmadenia macradenia* (Sond.) Dümmer and *Phyllosma barosmoides* (Dümmer) Williams.

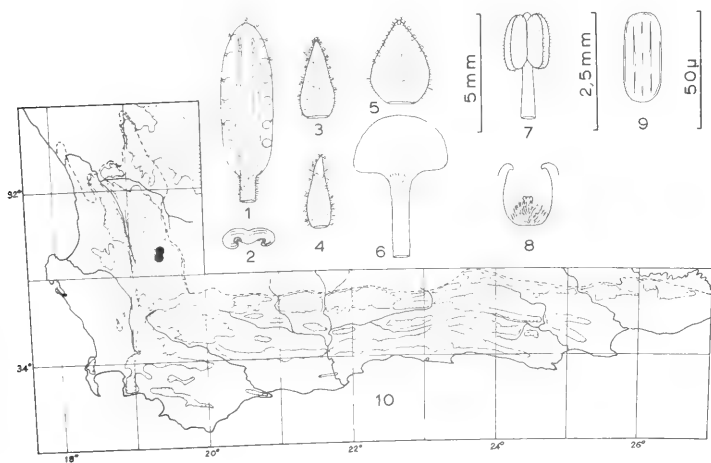


FIG. 4.

Sheilantha pubens: 1, leaf. 2, cross-section of leaf. 3, bract. 4, bracteole. 5, calyx lobe. 6, petal. 7, anther. 8, gynoecium with disc. 9, pollen. 10, distribution.



FIG. 5.

Sheilanthera pubens: Flower showing clawed petals and pubescent anthers.

THE FREQUENCY DISTRIBUTION OF B CHROMOSOMES IN A SOUTH AFRICAN CULTIVAR OF THE SWEETCORN "GOLDEN BANTAM"

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ABSTRACT

The frequency distribution of B chromosomes in a South African cultivar of the sweet-corn "Golden Bantam" differs significantly from that described previously in this variety. The possible significance of this is discussed.

UITTREKSEL

DIE FREKWENSIEVERSPREIDING VAN B CHROMOSOME IN 'N SUID-AFRIKAANSE KULTIVAR VAN DIE SUIKERMIELIE „GOLDEN BANTAM"

Die frekwensieverspreiding van B chromosome in 'n Suid-Afrikaanse kultivar van die suikermielie „Golden Bantam" verskil betekenisvol van wat voorheen vir die variëteit beskryf is. Die moontlike betekenis word bespreek.

INTRODUCTION

The diploid karyotype of maize consists of a standard complement of 10 pairs of A chromosomes, together with a variable number of B chromosomes. The B's are typically subtelocentric (Carlson, 1978) and relatively constant in size, although more variable types were recorded by early workers (Darlington & Upcott, 1941). The B's are highly heterochromatic, are subject to polarised non-disjunction at the second pollen grain mitosis, and are boosted in frequency within populations by preferential fertilisation of the B-containing male gametes (Roman, 1948). The effects of the B's include enhanced recombination (Rhoades, 1978) and the induction of sticking of the heterochromatic "knobs" of the A chromosomes at the anaphase of the second meiotic division resulting in the elimination of segments from the latter (Rhoades and Dempsey, 1973). The presence of B chromosomes has been used to trace the patterns of migration of maize races (McClintock, 1978).

However, relatively little attention has been paid to the frequency distribution of B chromosomes within varieties. Randolph (quoted in Darlington & Upcott, 1941) studied this aspect in four commercial varieties, and found that in two ("HG Nugget" and "Golden Bantam") the most frequent category of individual was that with one B chromosome, whereas in two others ("NYS Flint"

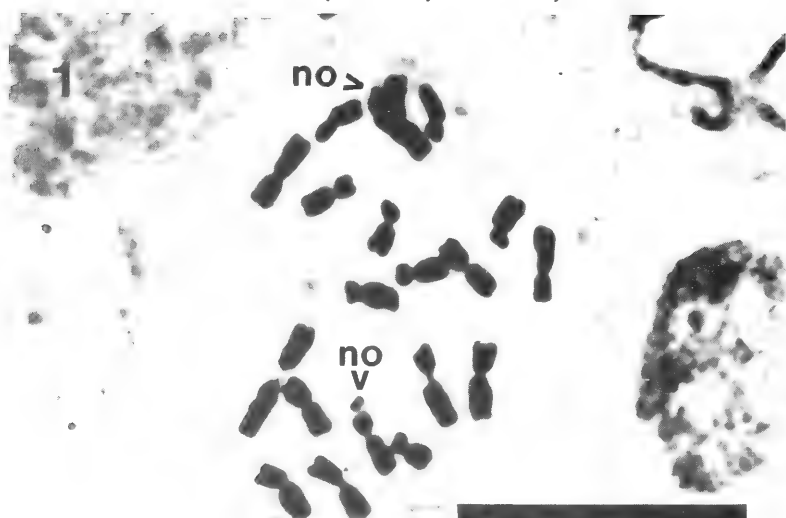


FIG. 1.
Somatic metaphase of a plant of *Zea mays* var. "Golden Bantam" possessing no B chromosomes. "no" indicates nucleolar organiser chromosomes, bar represents 10 μ .

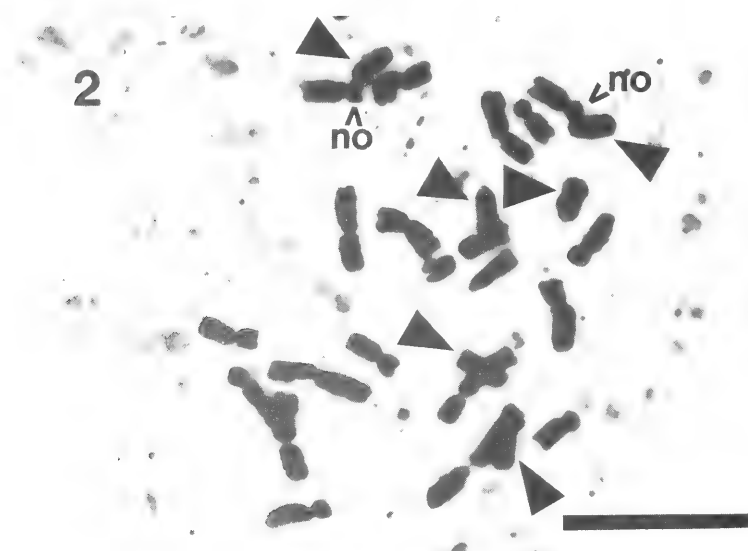


FIG. 2.
Somatic metaphase of a plant of *Zea mays* var. "Golden Bantam" possessing six B chromosomes (indicated by arrows). "no" indicates nucleolar organiser chromosomes, bar represents 10 μ .

and "Black Mexican") the most frequent categories were those with three and four B chromosomes respectively.

The present work consisted of a re-examination of B chromosome frequency in the variety "Golden Bantam", using a South African cultivar, to determine whether the frequency distribution in this cultivar differed from that described by Randolph.

MATERIAL AND METHODS

Seeds of the sweetcorn cultivar "Golden Bantam", obtained from MayFord Seeds (Johannesburg), were sown on moist filter paper in petri dishes at 24°C. Emergent radicles were pre-treated by incubation in a saturated aqueous solution of α -monobromonaphthalene for 4–5 hours at room temperature, and fixed in a 3:1 mixture of ethanol:glacial acetic acid overnight. The root tips were then hydrolysed in 1N HCl at 60°C for 6 minutes, softened by incubation in 5% aqueous cellulase for 2–3 hours, incubated in Schiff's reagent for 4–5 hours, and finally squashed in acetic orcein using an albumenised coverslip. The coverslip was then floated off in absolute ethanol, air-dried and mounted in Euparal.

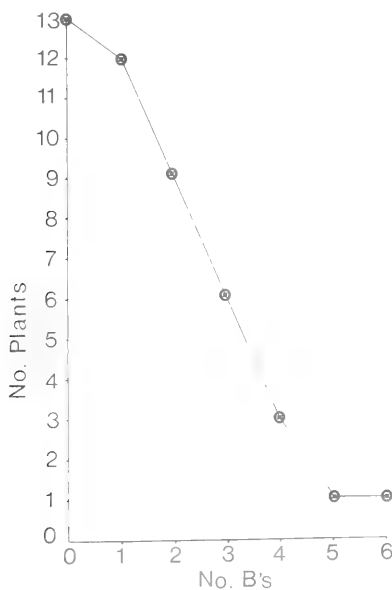


FIG. 3.

Frequency distribution of B chromosomes in the cultivar of *Zea mays* var. "Golden Bantam" studied.

RESULTS AND DISCUSSION

The cultivar was found to contain B chromosomes, which were of the normal subtelocentric type and which varied in number between plants from 0 to 6 (Figs 1, 2). The frequency distribution of B's constituted a curve of remarkable smoothness (Fig. 3), and differed from the previous result of Randolph in that the modal number of B's in the present case was nil rather than one.

It is therefore evident that the selective forces which maintain B chromosomes in maize do so in a manner which differs not only between varieties but also between different cultivars of the same variety. The work reaffirms that the frequency of B chromosomes is a selectively important element in the genetics of the variety, and emphasises that further breeding work on the variety could profitably include due consideration of their role.

ACKNOWLEDGEMENT

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MORFOLOGIE VAN DIE SPORODERM VAN *TYLOSEMA ESCULENTUM* EN *T. FASSOGLENSE*

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UITTREKSEL

Die kenmerke van die eksien van volwasse stuifmeel vind 'n belangrike toepassing in die taksonomie van blomplante en kan ook gebruik word om die Suid-Afrikaanse soorte van die genus *Tylosema* (Schweinf.) Torre & Hillc. van mekaar te onderskei. Geen opvallende verskille kon tussen die Suid-Afrikaanse *Tylosema*-soorte ten opsigte van hulle mikrospore en onvolwasse stuifmeelkorrels waargeneem word nie. Die belangrikste verskil berus op die seksienpatroon soos met behulp van die elektronmikroskoop gesien. Verskeie sitologiese kenmerke word geïllustreer.

ABSTRACT

MORPHOLOGY OF THE SPORODERM OF *TYLOSEMA ESCULENTUM* AND *T. FASSOGLENSE*

The characteristics of the pollen exine are important in the taxonomy of flowering plants and may also be used to distinguish between the species of the genus *Tylosema* (Schweinf.) Torre & Hillc. No marked differences occur between the microspores and young pollen grains of the South African species of *Tylosema*. The most important difference is based on the sexine structure as seen under the electron microscope. A number of cytological characteristics are illustrated.

INLEIDING

Die bestudering van stuifmeeleksien bring kenmerke na vore wat toepassing vind in dissiplines soos plantsitologie, plantbiochemie en veral die taksonomie van blomplante. Hierdie kenmerke is van groot belang in die taksonomie van blomplante omdat dit meesal baie konstante kenmerke is. Verskeie navorsers het al gepoog om op grond van die stuifmeelkenmerke, tussen planttaksons te onderskei soos ondermeer Schmitz (1973), Coetzee & Van der Schijff (1979) en andere soos blyk uit hierdie outeurs se literatuurlyste. So kan hierdie kenmerke ook by die genus *Tylosema* gebruik word om die soorte van mekaar te onderskei.

Die genus *Tylosema* ressorteer onder die familie Caesalpiniaceae van die orde Fabales en sluit vier soorte in waarvan slegs twee naamlik *T. esculentum* (Burch.) Schreiber en *T. fassoglense* (Schweinf.) Torre & Hillc. in Suidelike Afrika voorkom (Coetzer & Ross, 1977).

Al die soorte van die genus *Tylosema* is geofiete met 'n ondergrondse knol en bogrondse stingels wat kruipend of klimmend kan groei. Die blomme word in trosse gedra wat eindstandig op simpodiale vertakkings voorkom. Elke blom besit twee fertiele meeldrade en agt staminodiums. Die stuifmeel word vrygelaat wanneer die helmknoppe intrors met oorlangse splete open.

As gevolg van die verskeidenheid terme vir dieselfde begrippe wat in stuifmeelmorfologie gebruik word (Stanley & Linskens, 1974) is besluit om vir sover dit hierdie verslag aangaan, te volstaan by die terminologie van Erdtman (1956) soos aangepas deur Heslop-Harrison (1971).

MATERIAAL EN METODE VAN ONDERSOEK

Alle materiaal is naby Nelspruit, Groblersdal of Pretoria versamel in gebiede waar die plante natuurlik voorkom.

Vars helmknoppe asook helmknoppe wat vooraf in 'n formalien-asynsuur-alkoholmengsel (F.A.A.) gefikseer is, is volgens die metode van Erdtman (1966) geasetoliseer. Die behandelde stuifmeel is na aftaselektronmikroskoopknopies oorgedra, deur bedamping met 'n 30 nm-goudlagie bedek en met behulp van 'n Philips PSEM 501 elektronmikroskoop bestudeer.

Helmknoppe is uit blomknoppe van verskillende ouderdomme gedissekteer en in 6 % glutaraaldehid in 'n 0,05 mol. dm^{-3} natriumkaskodilaatbuffer van pH 7,4 gefikseer terwyl 2 % OsO_4 in dieselfde buffer vir die nafiksering van die materiaal gebruik is. Die dehidrering is met etanol en 1,2-propileenoksied gedoen en die inbedding met Spurr se inbedmedium en volgens sy metode (Spurr, 1969).

Die sneë is met behulp van 'n Reichert Om U3 ultramikrotroom en glasmesse gemaak. Die sneë is met 5 % uranielasetaat en loodsitraat gekleur (Reynolds, 1963). 'n Philips EM 301 elektronmikroskoop is vir die bestudering en foto-grafering van die sneë gebruik.

RESULTATE EN BESPREKING

Uitwendige bou van die stuifmeelkorrels

Die stuifmeel van die genus *Tylosema* is ellipties, monaad en apolêr. Die P/E-waarde vir *T. esculentum* is 1,41 en vir *T. fassoglense* 1,56 waar P en E onderskeidelik die lengte van die poolas en ekwatoriale as van 'n volwasse stuifmeelkorrel verteenwoordig. Hiervolgens is albei soorte stuifmeelkorrels se vorm prolaat, aldus Erdtman (1966). Die langste polêre as wat teengekom is, was 45 μm en die kortste as 33 μm , terwyl die langste en kortste ekwatoriale asse onderskeidelik 30 en 17 μm was.

Die gemiddelde lengtes wat waargeneem is, is soos volg:

T. esculentum P = 37,5 μm en E = 26,6 μm (Fig. 1).

T. fassoglense P = 42,2 μm en E = 27,0 μm (Fig. 2).



FIG. 1.

'n Stuifmeelkorrel van *T. esculentum* om die vorm daarvan en skulptuur van die eksien te toon. Skaalmerker = 10 μ m

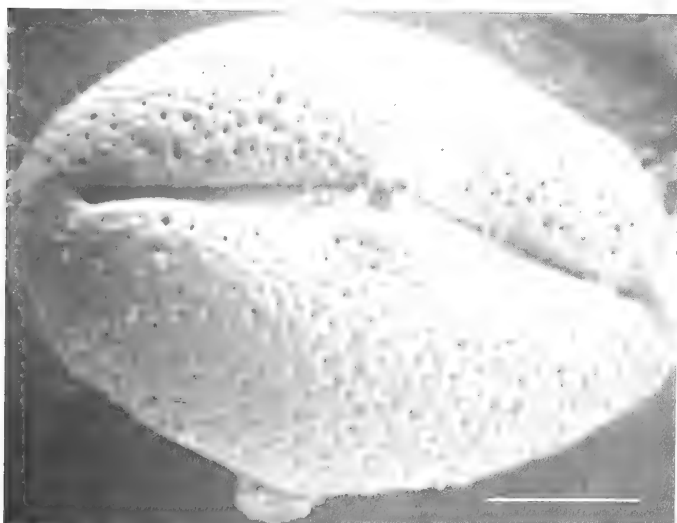


FIG. 2.

'n Stuifmeelkorrel van *T. fassoglense* om die vorm daarvan en die skulptuur van die eksien te toon. Skaalmerker = 10 μ m

Die ambitus van die *Tylosema*-stuifmeel is tri-aperturaat, en die stuifmeelkorrels as sodanig trikolporaat (Fig. 3). Die drie kolpiums is eweredig gespasieer en sluit ekwatoriaal drie min of meer ewegroot mesokolpiums in (Fig. 3). Die apokolpiums is duidelik afgebaken en slegs in uitsonderlike gevalle, waar die kolpiums by 'n pool anastomoseer, kom geen apokolpiums voor nie en is die stuifmeel sinkolpaat.

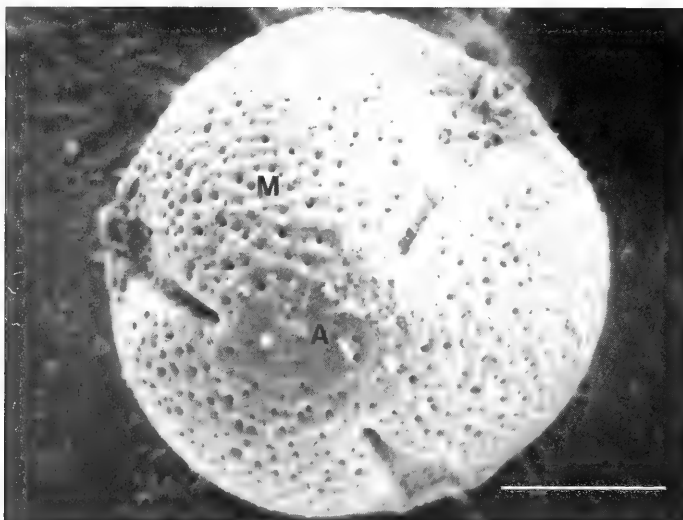


FIG. 3.

'n Stuifmeelkorrel van *T. esculentum* soos van 'n poolkant gesien. A = apokolpium; M = mesokolpium. Skaalmerker = 10 μ m

Die vorm en grootte van die kolpiums is taksonomies van waarde by die genus *Tylosema*. By *T. fassoglense* is die kolpiums ietwat vlakker en, volgens die lengte van P, in verhouding korter as by *T. esculentum*. Dit bring mee dat die apokolpiums by *T. esculentum* kleiner, minder gepunt en platter is as dié by *T. fassoglense*.

Morfologie van die sporoderm

Die wand van die stuifmeelkorrels bestaan uit 'n intien en 'n eksien wat in die meeste gevalle by volwasse stuifmeel duidelik van mekaar onderskei kan word. Die eksien by die *Tylosema*-soorte bestaan uit 'n duidelike seksien [ekteksien sensu Faegri & Iversen (1964)] wat saamgestel is uit 'n dik tektum en 'n

minder dik laag waar die bakulums en lumnas voorkom, en die neksien wat uit 'n minder opvallende neksien I en opvallend breë neksien II bestaan. Die intien is by jong stuifmeelkorrels baie dun of selfs afwesig en ontstaan op 'n later stadium as die eksien. Dit kan dan nie by jong stuifmeelkorrels waargeneem word nie (Fig. 4).

Kort nadat die mikrospore uit die tetrade vrygelaat word, bestaan hul eksien slegs uit 'n primeksien en kom die probakulums in die primeksien voor as meer elektron-digte dele wat op die meeste plekke terminaal verenig het om die tektum te vorm (Fig. 4). Voor die vrylating van die mikrospore verenig die probakulums op sommige plekke ook proksimaal om die neksien I, ook bekend as die voetlaag, te vorm.

Na vrylating uit die tetrade vergroot die mikrospore aansienlik. Heslop-Harrison (1971) rapporteer vir die genus *Lilium* 'n vergroting van 2,8 maal binne 24 uur na die tetrade opgebreek het. Hierdie vergroting het tot gevolg dat die primeksien dunner en yler word. Die seksien verkry verdere sporopollenien en die probakulums verdik sodat die sellulose-materiaal van die primeksien in die holtes tussen die probakulums vasgevang word (Fig. 4).

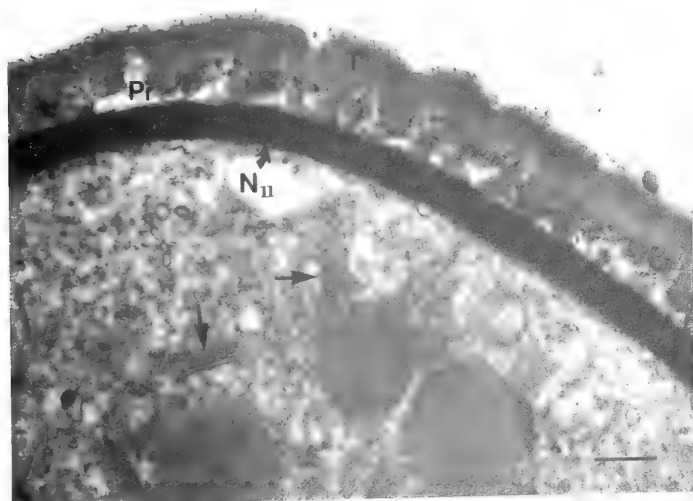


FIG. 4.

'n Deursnee deur 'n onvolwasse stuifmeelkorrel van *T. esculentum*. Let op die afwesigheid van 'n duidelike laag pollenkit. N_{II} = neksien II; Pr. = primeksien; T = tektum; pyltjies dui diktiosome aan. Skaalmerker = 1 µm

Sommige verslae (Rowley, 1963) wys daarop dat die eksien nie reeds vanaf die vroegste stadiums uit 'n homogene laag digte sporopollenien bestaan nie, maar dat dit aanvanklik uit bandvormige lagies van ongeveer 5 nm dik kan bestaan. Later konsolideer hierdie bande of lagies. Die konsolidering van die neksien II by die poriums vind egter laaste plaas. 'n Soortgelyke ontwikkeling is hier waargeneem (Fig. 5).

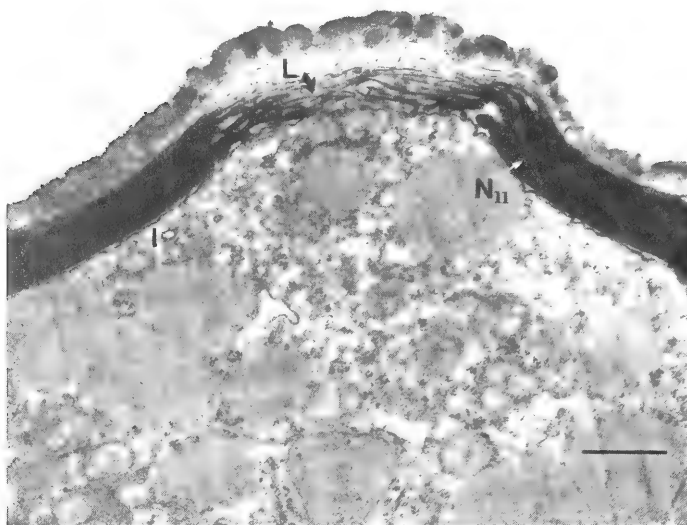


FIG. 5.

'n Deursnee deur 'n relatief jong stuifmeelkorrel van *T. esculentum* om die lamellas (L) van die neksien (N_{II}) in 'n poriumgebied te toon. Let op die jong intien (I) wat begin verskyn. Skaalmerker = 1 μ m.

Soos in dwarsnee gesien, is die tektum van die volwasse stuifmeelkorrels breër as die bakulumlaag plus die neksien I (Fig. 6). Omdat die bakulums gedurende die periode tussen vrylating uit die tetrad en antese aansienlik verdik as gevolg van die neerlegging van sporopollenien daarop, verklein meeste van die lumenas en vertoon die bakulums ook meesal oneweredig en nie meer pilaar- of staafvormig nie (Fig. 6 & 7). Die bakulums kom eweredig verspreid in die seksien voor en is nie in een of ander bepaalde orde gerangskik nie. Die distale en proksimale verdikking van die bakulums, wat die tektum en neksien I

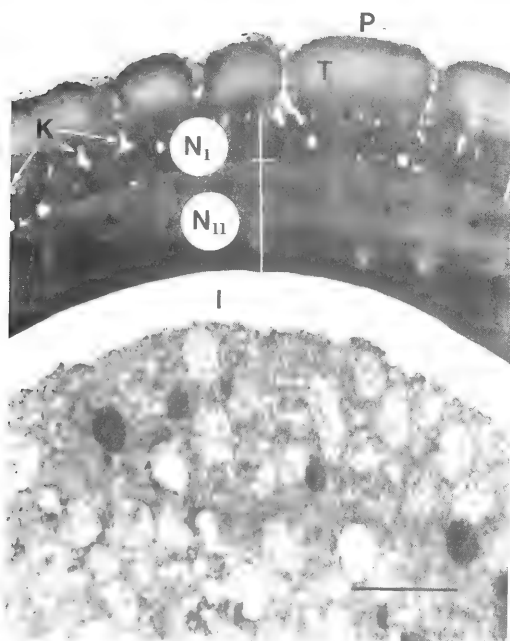


FIG. 6.

'n Deursnee deur 'n volwasse stuifmeelkorrel van *T. fassoglense* om die onderdele van die sporoderm en die relatiewe diktes van die lae te toon. Let op die dik tectum (T) en die pollenkit (P) wat op die tectum en in die tectumkanaaltjies voorkom. I = intien; K = lakunas; N_I = neksien I; N_{II} = neksien II. Skaalmerker = 1 μ m.

tot gevolg het, is nie sodanig dat aaneenlopende lae ontstaan nie want op sekere plekke kom openinge in beide die tectum en neksien I voor en is met die lumen in verbinding (Fig. 7). Hierdie openinge kom redelik reëlmatig verspreid op die mesokolpiums voor, maar is afwesig op die apokolpiums (Fig. 3).

Om die presiese oppervlakstruktuur van die eksien te bestudeer, is dit vooraf nodig om alle addisionale materiaal wat daarop mag voorkom, met behulp van die asetolise-proses van Erdtman (1966) te verwyder.

Die seksienpatroon van die sporoderm by die genus *Tylosema* is pertektaat omdat dit redelik glad en sonder prominente uitsteeksels is. Onder relatief lae



FIG. 7.

'n Bykans volwasse stuifmeelkorrel van *T. fassoglense* om 'n kolpium (K) soos in dwars-snee gesien, te toon. P = pollenkit. Skaalmerker = 1 μ m.

vergroting van ongeveer 1 000X vertoon die tektum 'n gelykmatige oneweredigheid met fyn holtes. By 10 000X en hoër vergroting egter vertoon die tektum van veral *T. esculentum*-stuifmeel baie meer oneweredig en vol porieë (Fig. 8 & 9). Die seksienpatroon is vir die genus *Tylosema* taksonomies van waarde omdat daar 'n konstante verskil in patroon tussen die stuifmeel van *T. esculentum* en *T. fassoglense* is.

Die tektum by *T. fassoglense* is taamlik homogeen verenig en vorm 'n relatief gladde oppervlak met reëlmatig verspreide porieë terwyl die tektum van *T. esculentum* meer oneweredig is met 'n verskeidenheid groottes porieë en langwerpige openinge (Fig. 8 & 9). Die volwasse stuifmeelkorrels is bedek met 'n eweredige laag tapetale afval, bekend as die pollenkit, wat meesal dien as 'n sement wat die korrels aan mekaar heg en gevolglik help by die bestuiwing van entomofiliese blomme (Hesse, 1979). Volgens Heslop-Harrison (1971) bestaan daar geen twyfel nie dat hierdie pollenkit by sommige stuifmeelsoorte 'n draer van belangrike stowwe is.

Opvallend by die genus *Tylosema* is die besonder dik neksien II wat aan die intien grens. By die kolpiums, uitgesonderd die poriums, word die seksien groot-

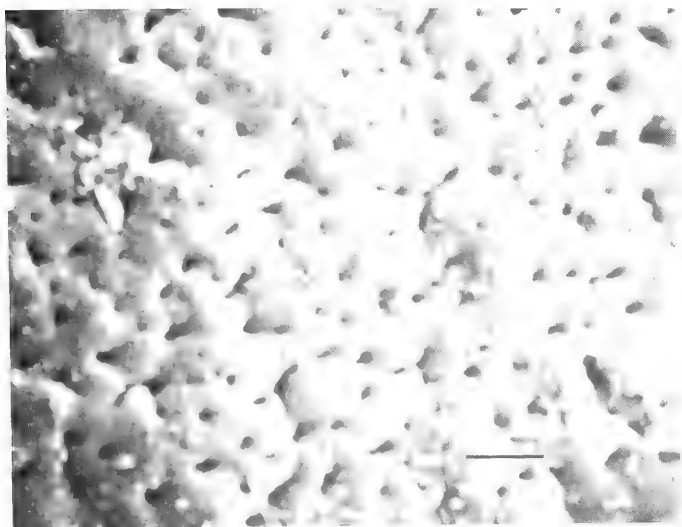


FIG. 8.

Die oppervlakskulptuur van 'n *T. esculentum*-stuifmeelkorrel. Skaalmerker = 1 μm .



FIG. 9.

Die oppervlakskulptuur van 'n *T. fassoglense*-stuifmeelkorrel. Skaalmerker = 1 μm .

liks onderbreek terwyl slegs die neksien II deurlopend voorkom (Fig. 7). By die porium in 'n kolpium word die hele eksien egter onderbreek en stulp die intien gedeeltelik na buite uit (Fig. 10). Lamellas, afkomstig van die endoplasmiese retikulum (ER), met sporopollenien, kan buite die intien waargeneem word (Fig. 10). Volgens Stanley & Linskens (1974) noem Saad (1963) hierdie los gelamelleerde laag die medien.

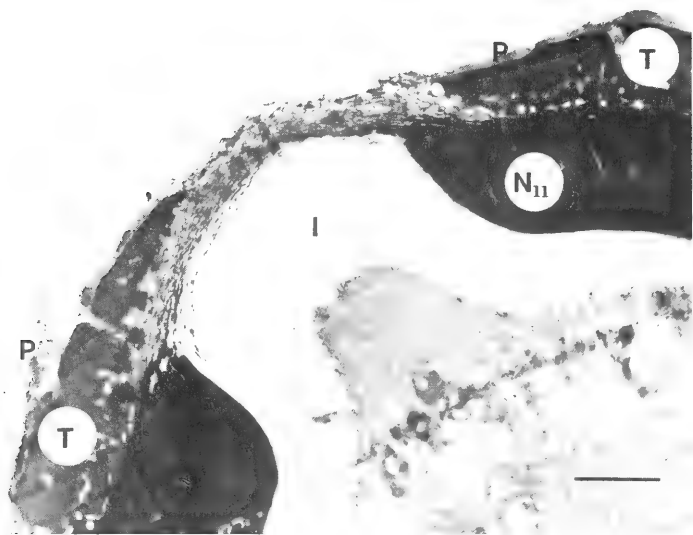


FIG. 10.

'n Deursnee van 'n *T. fassoglense*-stuifmeelkorrel om die bou van die sporoderm in 'n poriumgebied te toon. I = intien; N_{II} = neksien II; P = pollenkit; T = tektum. Skaalmerker = 1 μ m.

Alhoewel die neksien II (endeksien sensu Faegri & Iversen, 1964) ook uit 'n tipe sporopollenien bestaan (Heslop-Harrison, 1971), vertoon dit by volwasseheid elektronmikroskopies anders as die seksien en kan dit dus in die meeste gevalle maklik van die seksien onderskei word (Fig. 6, 7 & 10). Die vermoede bestaan dat die neksien II uit sporopollenien met 'n chemies-verskillende samestelling as dié van die seksien bestaan (Brooks & Shaw, 1977). Die materiaal van die neksien II kom skynbaar vanuit die mikrospoor self en dit akkumuleer deur die apposisie van lamellas aan die binnekant van die neksien I (Fig. 11). Soms

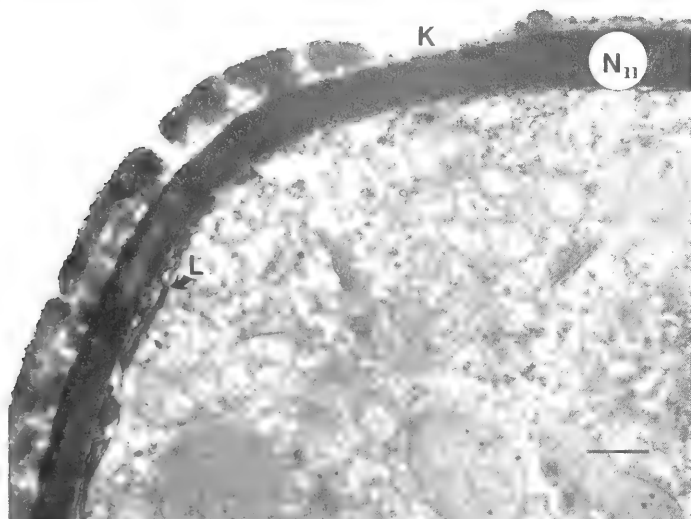


FIG. 11.

'n Deursnee van 'n *T. esculentum*-stuifmeelkorrel om die sporopolleniendragende lamellas (L) aan die binnekant van die neksten II (N_{II}) te toon. K = kolpiumgebied; T = tektum. Skaalmerker = 1 μ m.

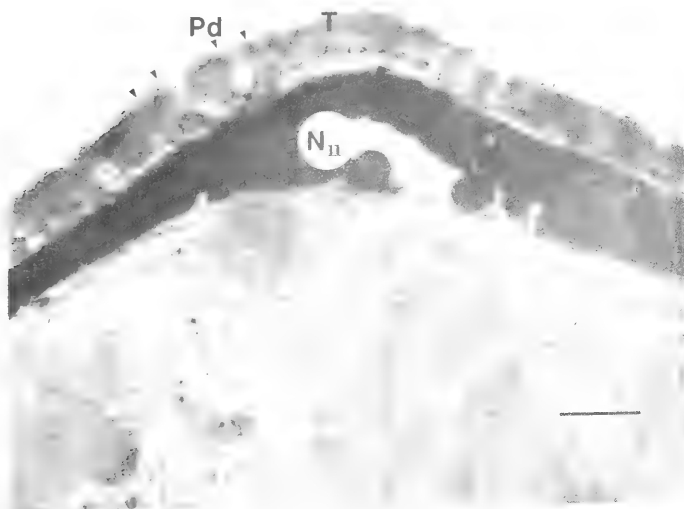


FIG. 12.

'n Deursnee van 'n *T. esculentum*-stuifmeelkorrel om die finale stadium in die konsolidering van die lamellas in die neksten II (N_{II}) te toon. Let op die fyn pollenkitdruppels (Pd) wat buite op die tektum (T) voorkom. Wit pyltjies dui neksten II-lamellas aan. Skaalmerker = 1 μ m.

kan die lamellas, voordat die sporopollenien gekonsolideer het, binne die neksien II (Fig. 5) of selfs aan sy buite-oppervlak waargeneem word (Fig. 12). Op sommige plekke word die neksien II ook dikker as die res van die eksien, veral naby die poriums (Fig. 10).

Die intien ontstaan eers nadat al die sporopollenien neergelê is (Stanley & Linskens, 1974). Diktosome is baie nou betrokke by die groei van die intien en kom redelik volop in die sitoplasma van jong stuifmeelkorrels voor (Fig. 4). By die *Tylosema*-soorte bereik die intien oor die grootste gedeelte van die oppervlakte van die stuifmeelkorrel 'n dikte van ongeveer helfte die dikte van die neksien II (Fig. 6), behalwe by die poriums waar dit opvallend breër word. Hier onderbreek dit die neksien en die grootste deel van die seksien, en stulp na buite uit (Fig. 10).

OPSOMMING

Alhoewel die mikrospore en baie jong stuifmeel van die *Tylosema*-soorte min, indien enige, taksonomies waardevolle kenmerke bied, kan *T. esculentum* en *T. fassoglense* maklik van mekaar onderskei word op grond van die seksienpatrone van die volwasse geasetoliseerde stuifmeel. Die seksienpatroon van die sporoderm is in albei gevalle pertektaat omdat die tektum 'n bykans gladde buite-oppervlak het sonder prominente uitsteeksels. Die pollenkit wat as 'n herkenbare lagie op die tektum voorkom, vul ook die openinge in die tektum en is taai en blywend. 'n Opvallend breë neksien II kom by die *Tylosema*-soorte voor en dit word slegs by die porium onderbreek waar die intien na buite uitstulp.

DANKBETUIGING

Hierdie navorsing is moontlik gemaak deur finansiële steun van die Universiteit van Pretoria en die W.N.N.R.

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA: 25-28

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25. *HAWORTHIA ANGUSTIFOLIA* Haw.

CHROMOSOME NUMBER: $2n = 14$ (Figs 1a, b).

ORIGIN OF MATERIAL: Woest Hill Pass, 3 km from Grahamstown, C.P. Rhodes University herbarium accession no. 24873 (RUH).

METHOD OF PREPARATION: Root tip material. Colchicine pretreatment, feulgen/acetic orcein staining.

OBSERVATIONS: A strongly bimodal karyotype. Very small, lightly straining regions are visible distally on the long arm of the longest chromosome pair of the large set, which by homology to the situation in *coarctata* and *reinwardtii* (see below) may be assumed to represent nucleolar organisers.

Tetraploids have been recorded in the species (Riley and Majumdar, 1979).

26. *HAWORTHIA COARCTATA* Haw.

CHROMOSOME NUMBER: $2n = 28$ (Figs 2a, b).

ORIGIN OF MATERIAL: 16 km from Grahamstown along Port Alfred road, C.P. Rhodes University herbarium accession no. 24874 (RUH).

METHOD OF PREPARATION: As in 25.

OBSERVATIONS: The karyotype resembles that of *angustifolia*, except that in the present species the nucleolar organiser and satellite regions are much more obvious.

The clone studied comprised tetraploid plants. Diploids and hexaploids have also been recorded (Riley and Majumdar, 1979).

27. *HAWORTHIA REINWARDTII* Haw.

CHROMOSOME NUMBER: a. $2n = 14$ (Figs 3a, b). b. $2n = 21$ (Fig. 4).

ORIGIN OF MATERIAL: a. Kaffir Drift, C.P. Rhodes University herbarium accession no. 24875 (RUH). b. Fraser's Camp, C.P. Rhodes University herbarium accession no. 24876 (RUH).

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FIG. 1A.
H. angustifolia, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

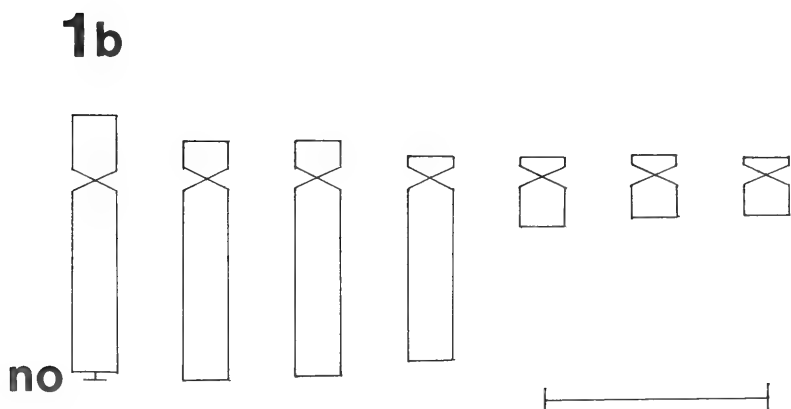


FIG. 1B.
H. angustifolia, haploid chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.



FIG. 2A.
H. coarctata, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

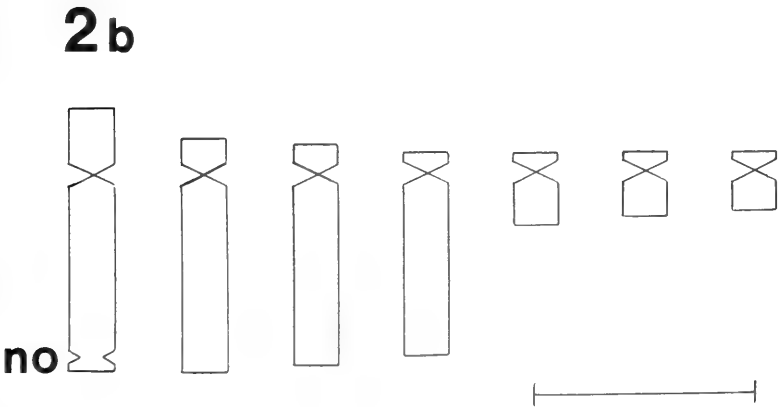


FIG. 2B.
H. coarctata, basic chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.



FIG. 3A.

H. reinwardtii, somatic metaphase of a diploid plant from Kaffir Drift. Bar represents 10 μ , arrows indicate secondary constrictions.

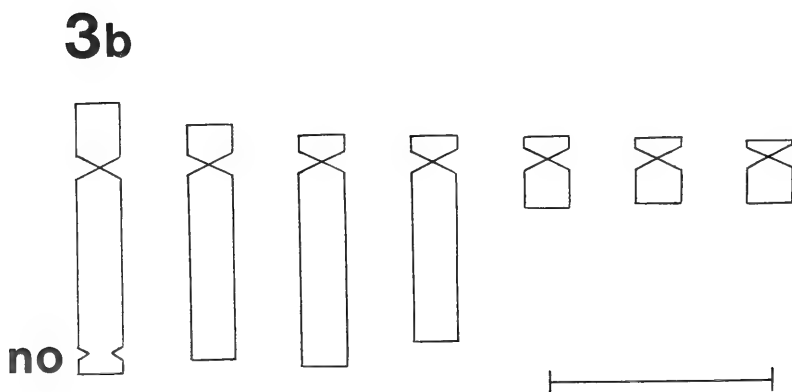


FIG. 3B.

H. reinwardtii, basic chromosome complement. Bar represents 10 μ , "no" indicates nucleolar organiser.



FIG. 4.
H. reinwardtii, somatic metaphase of a triploid plant from Fraser's Camp. Bar represents 10 μ , arrows indicate secondary constrictions.

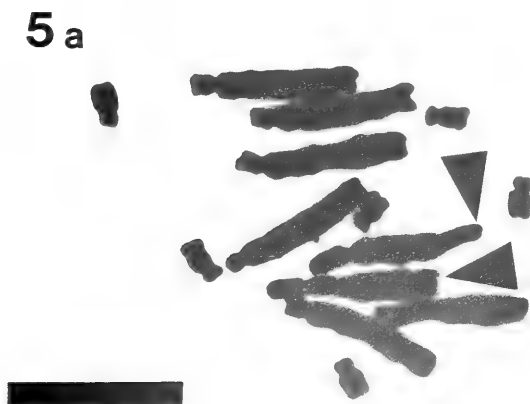


FIG. 5A.
H. translucens, somatic metaphase. Bar represents 10 μ , arrows indicate secondary constrictions.

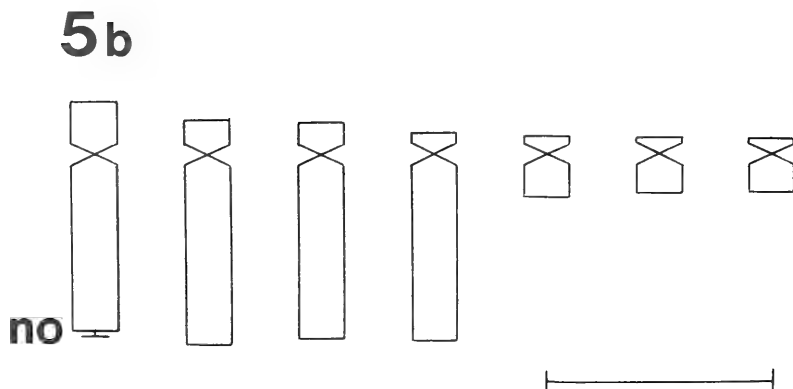


FIG. 5b.

H. translucens, haploid chromosome complement. Bar represents 10 μ, "no" indicates nucleolar organiser.

METHOD OF PREPARATION: As in 25.

OBSERVATIONS: The karyotype resembles that of *coarctata* in that conspicuous nucleolar organiser and satellite regions are present. Two such regions are visible in the diploid, three in the triploid.

In all three species so far described, extremely small terminal protruberances were occasionally observed distally on the long arms of large chromosomes other than those which bear the conspicuous nucleolar organiser and satellite regions referred to above. These may also represent such regions but were too small to permit consistent visualization.

Tetraploids have also been recorded in the species (Riley and Majumdar, 1979).

28. *HAWORTHIA TRANSLUCENS* Haw.

CHROMOSOME NUMBER: $2n = 14$ (Figs 5a, b).

ORIGIN OF MATERIAL: Hellspoort, nr. Grahamstown, C.P. Rhodes University accession no. 24877 (RUH).

METHOD OF PREPARATION: As in 25.

OBSERVATIONS: Nucleolar organiser and satellite regions very small as in *angustifolia*. Other protruberances of the type mentioned previously were not observed.

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THREE NEW SPECIES OF *HAWORTHIA* (LILIACEAE—ALOINEAE)

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ABSTRACT

Three new species and a variety of *Haworthia* are described. These are *H. bruynsii* Bayer from the Steytlerville area, which belongs in the sub-genus *Hexangulares* Uitewaal ex Bayer; *H. archeri* Bayer and *H. archeri* var. *dimorpha* Bayer from the Touws River—Matjiesfontein areas; and *H. rycroftiana* from the mid-Gouritz river valley.

UITTREKSEL

DRIE NUWE *HAWORTHIA* SOORTE (LILIACEAE—ALOINEAE)

Drie nuwe *Haworthia* soorte en 'n variëteit word beskryf. Dit is *H. bruynsii* Bayer van die Steytlerville-gebied, wat tot die subgenus *Hexangulares* Uitewaal ex Bayer behoort; *H. archeri* Bayer and *H. archeri* var. *dimorpha* Bayer van die Touwsrivier—Matjiesfontein area; en *H. rycroftiana* van die middel-Gouritzrivier vallei.

Haworthia bruynsii Bayer, sp.nov. (Liliaceae—Aloineae)

Rosula acaulescente, 40–70 mm diam. foliis usque ad 11. *Caule* usque ad 20 mm diam., non proliferante. *Foliis* erectis, usque ad 30 mm in longitudine, 14 mm in latitudine, 10 mm in crassitie cum area extremitatis truncata, obtusa; *ventrale pagina* leviter concava, brunnea-viride, laeve non lineata, supra tuberculis pallidis roseis, area truncata et marginibus scabris, opaca usque ad 3 striolis roseis pallidis; *dorsale pagina* convexa, nonlineata, brunnea-viride apice roseis papillatis, carinata minute; *marginibus* acutis, integris. *Pedunculo* singulare, 1–1,5 mm diam., 250–450 mm in longitudine cum racemo, cano-brunneo; *racemo* 150–250 mm in longitudine, 9–23 floribus fere secundis, 2–4 simul apertis; *Perianthio* cano-viride et albo, 15 mm longo, perigonio rotundo, segmentis superis-exterioribus rectis, segmentis interioribus-inferioribus cum marginibus involutis et recurvis apicibus expansis, *tubo* pallide viride; *gemma* angusta, recta, decurvata apice leviter.

Rosette acaulescent, 40–70 mm diam., up to 11 leaves. *Stem* up to 20 mm diam., non-proliferous. *Leaves* erect up to 30 mm long, 14 mm wide, 10 mm thick with truncated, obtuse end-area; *face* slightly concave, brownish-green, smooth unlined, pinkish tubercles above, truncated area and margins scabrid,



FIG. 1.
Haworthia bruynsii Bayer.

opaque with up to 3 inconspicuous pinkish longitudinal lines; *back* convex, unlined, brownish-green, with apical pinkish tubercles, minutely keeled at apex; *margins* acute, entire. *Peduncle* single, 1–1.5 mm diam., 250–450 mm long including raceme, greyish-brown; *raceme* 150–250 mm long, with 9–23 nearly secund flowers, 2–4 open at a time, petioles 3–5 mm long. *Perianth* greyish-green and white, 15 mm long, perigon rounded, upper-outer segments straight, inner-lower segments with involuted margins and recurved, tips flared, *tube* pale green, *bud* narrow, straight, slightly down-curved at tip. *Flowering* December–January.

Type: CAPE—3324 (Steytlerville): 20 km south-east of Steytlerville, *G. J. Rossouw* 456 (NBG, holo.).

This is a most remarkable species particularly in respect of its flower. When first collected by Mr P. V. Bruyns after whom it is named, the single plant was considered perhaps to be an ecotypic variant of *H. springbokvlakensis* Scott. The latter species is itself remarkable as it is the most easterly of the “retuse” species in the sub-genus *Haworthia* Uitewaal ex Bayer. It is found east of Steytlerville, and although its flower is very similar to that of *H. comptoniana* Smith

and *H. emelyae* v. Poelln. at Georgida and Uniondale respectively, there appears to be no intermediate population. The origin and identity of *H. willowmorensis* v. Poelln. is very dubious and unlikely to be resolved.

Thus the collection of *H. bruynsii*, west of *H. springbokvlakensis*, and belonging in the sub-genus *Hexangulares* is extraordinary. The flowers are practically secund, the florets are widely spaced on a relatively slender, wiry peduncle, the margins of the outer perianth lobes are well-separated and, fused with the outer surfaces of the inner perianth lobes. The perianth base is regularly 6-sided and the tube is straight. The species which occur in the same general area are *H. viscosa* (L.) Haw., *H. nigra* (Haw.) Baker, *H. woolleyii* v. Poelln., *H. sordida* (Haw.), *H. glauca* Baker var. *herrei* (v. Poelln.) Bayer (in the sub-genus *Hexangulares*) and *H. decipiens* v. Poelln., *H. springbokvlakensis* and *H. zantneriana* v. Poelln. (sub-genus *Haworthia*). There is nothing to suggest that it is a hybrid and its occurrence in at least two distinct, discrete populations discounts this as well. The locality of Steytlerville is possibly at the epicentre of distribution of the genus, and the oddity of the species may be relevant to the origin of the sub-genera.

OTHER SPECIMENS EXAMINED

CAPE—3324 (Steytlerville): 10 km south-east of Steytlerville, G. J. Rossouw 450 (NBG).

Haworthia archeri W. F. Barker ex M. B. Bayer, sp. nov. (Liliaceae—Aloineae)

Rosula acaulescente, 40–60 mm diam., *foliis* usque ad 120. *Caule* usque ad 10 mm diam., non proliferante. *Foliis* expansis usque ad erectis, usque ad 26 mm longis, 5 mm latis, 2 mm crassis, apicibus incurvis, arista apice 2 mm longa; *ventrale pagina* convexa, armata 1–2 seriebus dentium minorum in triente supero; *dorsale pagina* convexa 1–3 seriebus dentium minorum in dimidio supero; *marginibus* supra dentibus minutis. *Pedunculo* singulare 1–1.5 mm diam., 300–500 mm longo cum racemo. brunneo-viride; *base* laeve perangusta elliptica; *racemo* 10–15 floribus, 3–4 simul apertis; *pedicellis* longis usque ad 7 mm, 1 mm diam.; *bracteis* sterilibus 12–15, 6–7 mm in longitudine. *Perianthio* viride et albo, 16 mm longo, perigonio sub-triangulari, segmentis superis-exterioribus rectis, interioribus-superis fere rectis; *tubo* interno pallido viride; *gemma* apice rotundato.

Rosette acaulescent, 40–60 mm diam., up to 120 leaves. *Stem* up to 10 mm diam., non-proliferous. *Leaves* spreading to erect, up to 26 mm long, 5 mm wide, 2 mm thick, with incurved tips and 2 mm long end-awns; *face* convex with 1–2 rows of minute teeth on upper third; *back* convex with 1–3 rows of minute teeth on upper half; *margins* minutely toothed above. *Peduncle* single, 1–1.5



FIG. 2.

Haworthia archeri W. Barker ex Bayer.

mm diam., 300–500 mm long including raceme, brownish-green; *base* smooth, very narrowly elliptic; *raceme* with 10–15 flowers, 3–4 open at a time; *pedicels* up to 7 mm long, 1 mm diam., *sterile bracts* 12–15, 6–7 mm long. *Perianth* green and white, 16 mm long, perigon sub-triangular, upper-outer segments straight and inner-upper segment nearly so; *tube* pale green inside; *buds* with rounded tip. *Flowering* February.

Type: CAPE—3320 (Montagu): Whitehill (–BA), *J. Archer s.n.*, NBG 68145 (NBG, holo.).

Mr J. Archer, in whose honour this species is named, was the first curator of the Karoo Botanic Garden from when it was founded at Whitehill near Laingsburg in 1921.

It had apparently never been re-collected until Mr P. V. Bruyns found it in 1977. It is a small compact brownish-green species apparently belonging in the *H. magnifica* group. However, this latter species is a constituent of the south-western Cape complex. Although comprised of highly localised, variable and

intergrading elements, *H. magnifica* v. Poelln. can be defined in geographical terms. *H. magnifica* is also recognised by its 'fish-tail' tips to the buds. It is not known north of the Langeberg mountains except at Garcia's Pass, Barrydale and Montagu. *H. archeri* does not have the flowers typical of its south-western Cape relatives and is separated from *H. magnifica* by the wide valley of the Touws River, and the very broken country of the Warmwaterberg, Anysberg and Witteberg ranges. Epidermal structure has not been studied in this group but the cells are sharply papillate, compared to the more dome-shaped cells in *H. magnifica*.

Affinity, unlikely as it seems, can only be sought with *H. marumiana* Uitevaal, which is a very widespread species, localised in habitat and generally poorly known. It is known to occur in the Nuweveld Mountains at Beaufort West, across the mountains of the central Karoo to Tarkastad.

A particularly spiny form of *H. arachnoidea* (L.) Duv. occurs together with *H. archeri*. *H. lockwoodii* v. Poelln. is a quite different species occurring together with *H. wittebergensis* Smith about 10 km to the south.

OTHER SPECIMENS EXAMINED

CAPE—3320 (Montagu): Baviaan, W. Laingsburg (—BA), *P. V. Bruyns 1405* (NBG); Ngaap Kop, W. Laingsburg, *P. V. Bruyns 1664* (NBG).

***Haworthia archeri* M. B. Bayer var. *dimorpha* M. B. Bayer, var. nov.**
(Liliaceae—Aloineae)

Rosula 40–50 mm diam., foliis 15–25, non proliferante. *Foliis* erectis usque ad 40 mm longis, 10 mm latis, 3 mm crassis, arista apice 5 mm longa; *ventrale pagina* convexa dentibus paucis in rotundatis, pellucidis punctis; *dorsale pagina* convexa 1–2 seriebus dentium 1 mm longorum, carinata; *marginibus* dentatibus supra cum albis dentibus translucentibus, 1 mm longis.

Rosette 40–50 mm diam., with 15–25 leaves, non-proliferous. *Leaves* erect up to 40 mm long, 10 mm wide, 3 mm thick with 5 mm long end-awn; *face* convex with a few scattered teeth on rounded clear dots; *back* convex with 1–2 rows of 1 mm long teeth, keeled; margins toothed above with white, translucent 1 mm long teeth.

Type: CAPE—3320 (Montagu): 14 km east of Touws River, *M. B. Bayer 2092* (NBG, hol.).

Unlike the typical variety which occurs in karroid vegetation on Witteberg quartzites, *H. archeri* var. *dimorpha* occurs in fynbos on Table Mountain sandstone. The name is derived from the extraordinary transformation observed in cultivated specimens. These doubled in size with broad flatter, recurving leaves



FIG. 3.

Haworthia archeri W. Barker ex Bayer var. *dimorpha* Bayer.

and large clear teeth. The affinity with *H. archeri* is deduced from the flower which also has the same straight upper perianth lobes, and from the locality some 30 km to the west of the species. The Touws River area is relatively poor in *Haworthia*. Even *H. venosa* (Lam.) Haw. is very poorly represented by aberrant forms more closely allied to the subspecies, *H. venosa* (Lam.) Haw. subsp. *granulata* (Marloth) Bayer.

H. arachnoidea does occur south of Touws River where identification is in fact a little dubious as here this species is a very dark green somewhat resembling *H. unicolor* v. Poelln. var. *venteri* (v. Poelln.) Bayer. The nearest species geographically is *H. pulchella* Bayer, south-east of Konstabel Station and south of Touws River itself. This species has a rather coriaceous texture and a direct affinity is unlikely.

OTHER SPECIMENS EXAMINED

CAPE—3320 (Montagu): Constable Station, W. Laingsburg (—AD), *H. Hall* sub *G. G. Smith* 7418 (NBG).

Haworthia rycroftiana M. B. Bayer, sp. nov. (Liliaceae-Aloineae)

Rosula acaulescente, 50–80 mm diam., foliis usque ad 50. *Caule* usque ad 12 mm diam., proliferante. *Foliis* erectis, usque ad 50 mm longis, 18 mm latis, 6 mm crassis, apicibus incurvis, arista apice 10 mm longa; *ventrale pagina* convexa, laevigata, inconspice reticulate; *dorsale pagina* convexa, laevigata, supra modice carinata, inconspice reticulate. *Pedunculo* singulare, 2 mm diam., 250–300 mm longo cum racemo brunneo-viride; *base* laeve, 5–7 angulate; *racemo* 12–20 floribus, 3–5 simul apertis; *pedicellis* longis usque ad 7 mm, < 1 mm diam.; *bracteis sterilibus* 7–8, 4–5 mm in longitudine. *Perianthio* brunneo-viride et albo, 13 mm longo, perigonio triangulare, segmentis patentia; *tubo* interno brunneo-viride; *gemma* apice acumen breviate.

Rosette acaulescent, 50–80 mm diam., up to 50 leaves. *Stem* up to 12 mm, proliferous. *Leaves* erect, up to 50 mm long, 18 mm wide, 6 mm thick, with acuminate incurved tips and 10 mm long end-awns; *face* convex, smooth, faintly reticulate; *back* convex; smooth, lightly keeled above, faintly reticulate. *Peduncle* single, 2 mm diam., 250–300 mm long including raceme, brownish-green; *base* smooth, 5–7 angled; *raceme* with 12–20 flowers, 3–5 open at a time; *pedicels* up to 7 mm long, < 1 mm diam.; *sterile bracts* 7–8, 4–5 mm long. *Perianth* brownish-green and white, 13 mm long, perigon triangular, segments spreading; *tube* brownish-green inside; *buds* with short pointed tips. *Flowering* December-January.

Type: CAPE—3321 (Ladismith): Gouritz River between Van Wyksdorp and Herbertsdale (–DC), *M. B. Bayer 1701* (NBG, holo.).

This species is named in honour of Prof. H. B. Rycroft, Director of the National Botanic Gardens of South Africa. *H. turgida* Haw. occurs in the mid-Gouritz River valley and this new species appears to represent an unexpected link between that species and *H. unicolor* v. Poelln. which occurs in the south-western Little Karoo. Both *H. unicolor* v. Poelln. var. *venteri* (v. Poelln.) M. B. Bayer and *H. habdomadis* var. *morrisiae* (v. Poelln.) M. B. Bayer occur sympatrically 10 km south of Vanwyksdorp (hairy and smooth species respectively), and *H. rycroftiana* has similarities. However, the turgidity of the leaves, the fewer-flowered raceme with more pointed bud-tips, together with its proliferous nature, clearly separate it.

A COMPARISON OF THE SEASONAL GROWTH OF INDIGENOUS AND NON-INDIGENOUS SPECIES IN THE SOUTH-WESTERN CAPE

J. E. M. SOMMERVILLE

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ABSTRACT

The shoot growth of four indigenous and five non-indigenous species was investigated at a coastal and a montane site in the South-Western Cape. Forty shoots of each species were labelled and measured at monthly intervals over a period of 12 months. The results were similar to those of Specht (1973, 1975) who observed that non-indigenous *Pinus radiata* and a *Lolium* species exhibit vegetative growth flushes before dominant indigenous South Australian species. Specht suggests that this early growth flush contributes to the invasive success of both *Pinus* and *Lolium*. *Pinus* and *Lolium* are Mediterranean species and their phenology is markedly different from the Australian species. The difference in shooting phenology of the Australian invasive species and four South-Western Cape species studied is not as marked. Nevertheless, the five non-indigenous species exhibit shoot growth peaks slightly before the four indigenous species and this may contribute to their successful invasion of the South-Western Cape vegetation.

UITTREKSEL

'N VERGELYKING VAN DIE SEISOENALE GROEI VAN IN- EN UITHEEMSE SOORTE IN DIE SUID-WESTELIKE KAAP

Die groei van lote van vier inheemse en vyf uitheemse soorte was ondersoek by 'n kus en berg terrein in die Suid-Westelike Kaap. Veertig lote van elke soort is gemerk en maandeliks gemeet oor 'n periode van 12 maande. Die resultate was soortgelyk aan die van Specht (1973, 1975) wat waargeneem het dat *Pinus radiata* en *Lolium* soorte vegetatiewe groeivermeerdering voor die dominante inheemse Suid-Australiese soorte vertoon. Specht stel voor dat die vroeë groeivermeerdering bydra tot die indringende sukses van beide *Pinus* en *Lolium*. *Pinus* en *Lolium* is Mediterreense soorte en hul fenologie is merkbaar anders as die Australiese soorte. Die verskille tussen die lootfenologie tussen die vyf indringer Australiese soorte en die vier Suid-Westelike Kaapse soorte wat bestudeer is, is nie groot nie. Die vyf uitheemse soorte vertoon egter 'n lootgroei piek effens voor die vier inheemse soorte en dit mag bydra tot hul suksesvolle indringing in die Suid-Westelike Kaapse plantegroei.

INTRODUCTION

This investigation was stimulated by Specht's work on seasonal growth patterns exhibited by plants in the mediterranean region of South Australia. Specht observed late spring and summer shoot growth peaks in the dominant indigenous tree, shrub and perennial grass species (Specht 1973, 1975). Both *Pinus radiata* and *Lolium* sp. which are non-indigenous, mediterranean species, exhibited growth peaks during late winter and spring. Specht concluded "the radiata pine trees thus have a strong competitive advantage over native eucalypts in being in a position to make maximum use of limited resources of both nutrients

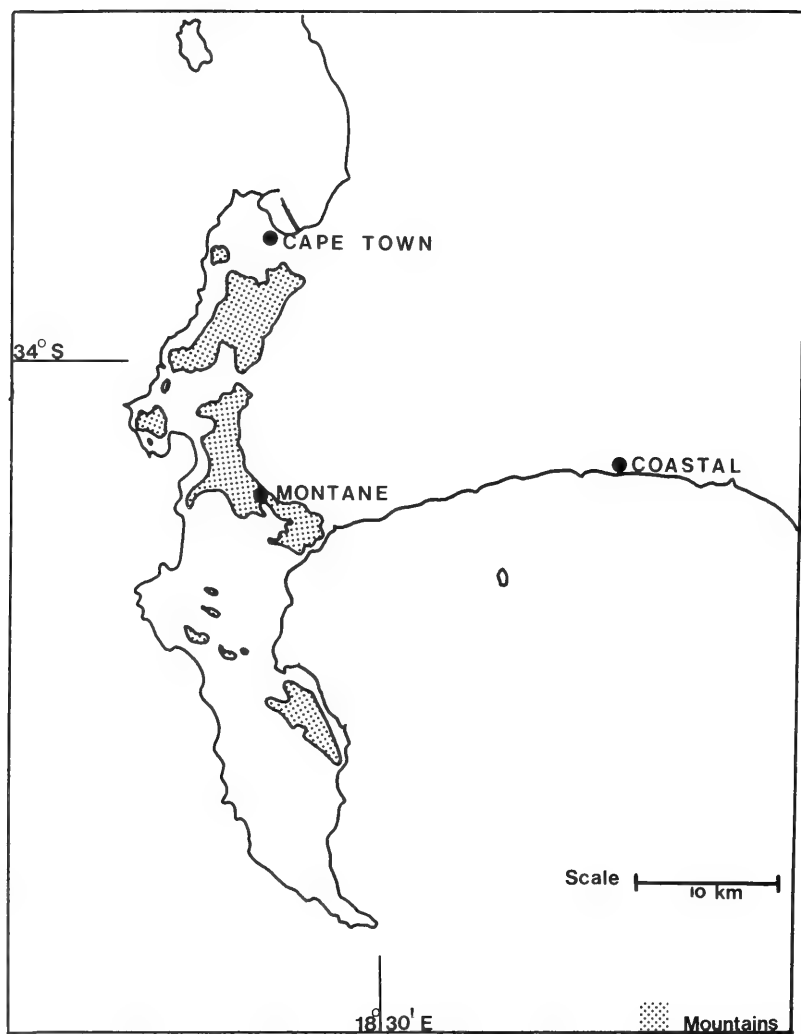


FIG. 1
Map of the Cape Peninsula and environs showing the two study sites.

and water in canopy growth in spring, some months before the native species" (Specht, 1975).

The aim of this study was to investigate whether the same growth pattern held true for several non-indigenous species in the South-Western Cape but no attempt was made to test his conclusions.

Study sites

The study sites, one coastal and one montane (Figure 1), were chosen because they supported both non-indigenous and indigenous species rather than dense non-indigenous stands.

The coastal site was on deep sand and subject to strong SE onshore winds. The montane site was on shallow rocky, sandy loam and experiences greater temperature fluctuations and higher precipitation (Figure 2).

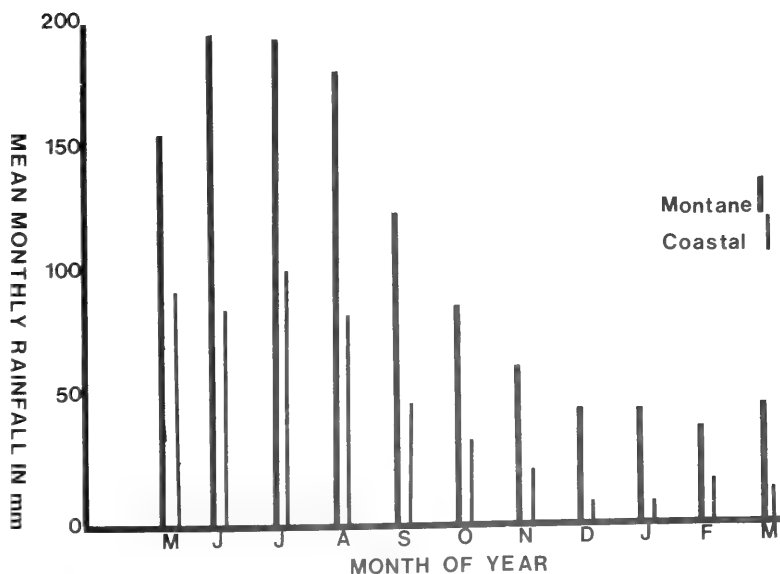


FIG. 2

Mean monthly rainfall data for Silvermine, montane (Cape Town City Council Waterworks, pers. comm., 1980) and D. F. Malan, coastal (Weather Bureau, 1965).

Species investigated

Five common non-indigenous shrub or tree species, two Australian acacias, two hakeas and the mediterranean species *Pinus pinaster* were investigated. The acacias have essentially invaded large lowland areas and the *Hakea* and *Pinus* species montane areas (Stirton, 1978). Four common indigenous shrub species were selected for the suitability of their shoots for labelling and measurement.

TABLE 1.
Species investigated

Species	Coastal Site	Montane Site
<i>Non-Indigenous</i>		
<i>Acacia cyclops</i> A. Cunn. ex G. Don.	✓✓*	✓
<i>A. saligna</i> (Labill.) Wendl.		✓
<i>Hakea gibbosa</i> (Sm.) Cav.		✓
<i>H. sericea</i> Schrad.		✓
<i>Pinus pinaster</i> Ait.		✓
<i>Indigenous</i>		
<i>Berzelia lanuginosa</i> Brongn.		✓
<i>Colpoon compressum</i> Berg.	✓	✓
<i>Myrica cordifolia</i> L.	✓	
<i>Rhus lucida</i> L.	✓	✓

* An exposed and a sheltered individual.

Measurement of relative growth rates

Forty shoots of each species were labelled and measured at approximately monthly intervals from April 1976 to March 1977. Monthly growth was calculated as a percentage of the original length and expressed as a daily rate. A mean shoot elongation rate was calculated for each species.

RESULTS

Figures 3–10 show the mean daily shoot elongation rates each month for the 13 study plants. Table 2 below summarizes the results.

Hakea sericea exhibited a growth peak during August–September (late winter to early spring), (Figure 3).

Both coastal examples of *Acacia cyclops* showed maximum growth rates during spring (September–November), (Figure 4). The exposed individual was severely sheared by the salt and sand-bearing winds; this shearing accounts for the lower shoot elongation rate of this plant compared with the sheltered plant. The windward shoots were long and unbranched, presumably to compensate for

TABLE 2.
Periods of maximum shoot growth

Species	A	S	O	N	D	J	F	M	A	M	J	J
<i>Hakea sericea</i> *	_____											
<i>Acacia cyclops</i> * (coastal)		_____										
<i>Hakea gibbosa</i> *			_____				_____					
<i>Pinus pinaster</i> *				_____								
<i>Acacia saligna</i> *				_____								
<i>Berzelia lanuginosa</i>				_____								
<i>Myrica cordifolia</i>					_____							
<i>Colpoon compressum</i> (coastal)						_____						
(montane)								_____				

* non-indigenous species

the frequent shearing of the tips. The leeward tips were short and much branched. The sheltered individual was taller and not as densely branched as the other. *Acacia cyclops* is most common on the calcareous sands of the Cape Flats (Milton, 1980). The montane example on a sandstone slope appeared to be less vigorous with a lot of dead wood and was apparently in a marginal habitat. For this reason it had a low growth rate as compared with the coastal examples.

Hakea gibbosa showed two small growth peaks in October (spring) and February (late summer), (Figure 3).

Pinus pinaster exhibited slow shoot elongation with a peak in November—December (late spring to early summer), (Figure 5).

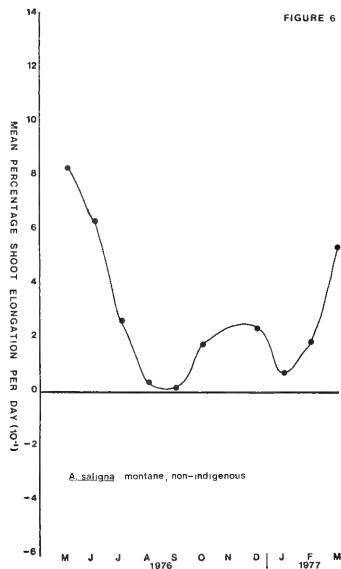
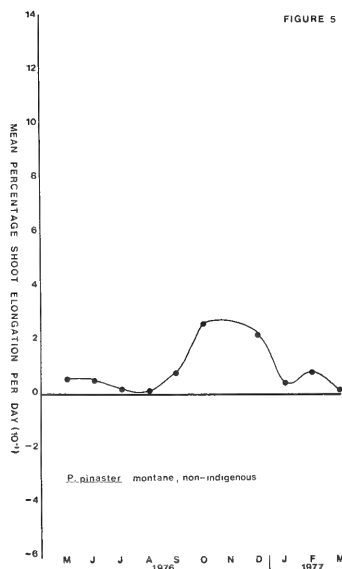
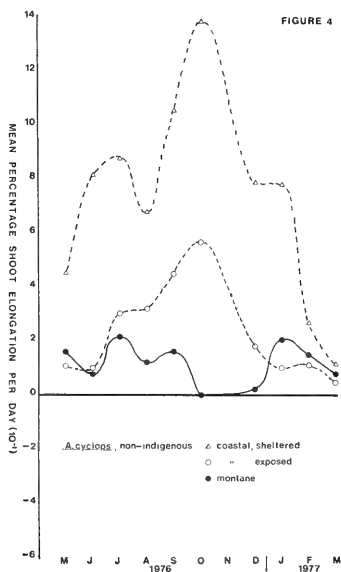
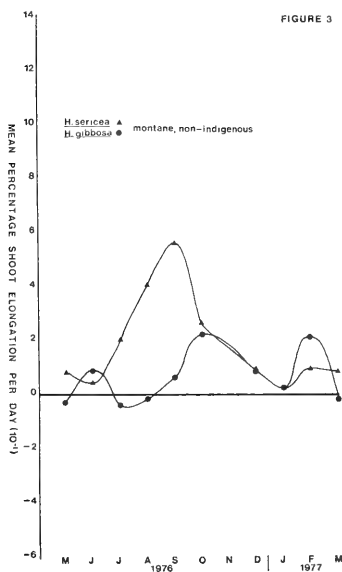
Acacia saligna had an obvious growth peak during autumn (March—May) with a slight increase during November—December (late spring to early summer), (Figure 6). The major growth flush is not during late winter to early summer like the other four alien species. But this growth flush is due to the production of peduncles which do not constitute true vegetative growth. The November—December peak is a vegetative growth flush.

Berzelia lanuginosa exhibited a shoot growth peak during November—January (late spring to early summer), (Figure 7), similar to *A. saligna* and *P. pinaster*.

Myrica cordifolia grew most rapidly during summer (December—February), (Figure 8).

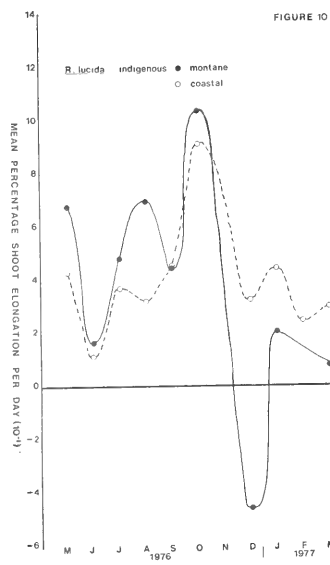
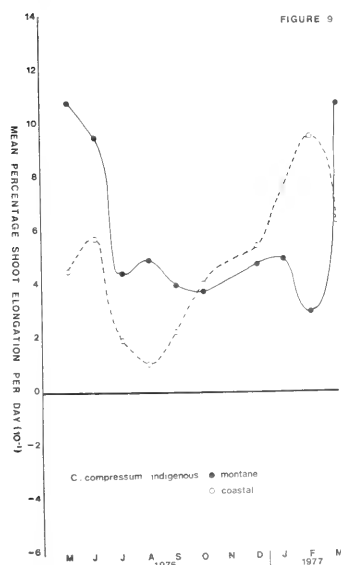
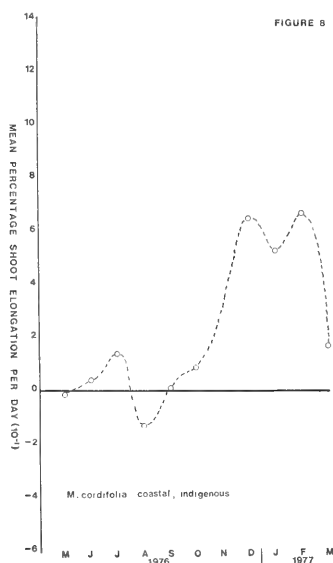
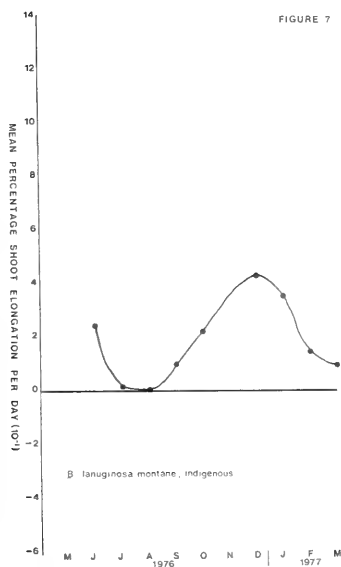
The coastal example of *Colpoon compressum* exhibited a summer growth peak during January and February. The montane example exhibited maximum growth later during autumn (March—May), (Figure 9). This suggests that the growth rhythm is affected by environment and is not genetically fixed.

Rhus lucida was unsuitable for this method of growth measurement. Like *A.*



FIGS 3-6

Mean daily shoot elongation, expressed as a percentage of shoot length the previous month, at approximately monthly intervals.



FIGS 7-10

Mean daily shoot elongation, expressed as a percentage of shoot length the previous month, at approximately monthly intervals.

saligna it has long peduncles which are not strictly vegetative shoots. After flowering during September and October these shoots die and shrivel, or fall off. This explains the negative growth of the montane individual during December, (Figure 10). But I could not distinguish a vegetative growth peak from this peduncle growth as I did for *A. saligna*.

DISCUSSION

In studying shoot growth in this manner two assumptions were made. Firstly, shoot elongation is evidence of increased uptake of water and/or nutrients. Secondly, shoot elongation is an index of increased photosynthetic area. But in the first instance there may be a difference in the lag between uptake and conversion to shoot elongation in different species. In addition current shoot growth may be utilising stored carbohydrates (Groves, 1965; Specht, 1975). The second assumption was not tested, again there may be different lag phases between shoot growth and leaf expansion.

Table 2 and Figures 3–10 show that the non-indigenous species investigated exhibit shoot growth peaks slightly earlier than the indigenous species. I assume that this affords them some competitive, photosynthetic advantage which allows non-indigenous species to out-compete the indigenous species by precocious uptake of water and/or nutrients. To extend this to other communities one must further assume that the indigenous species studied are representative of these communities too. It must also be assumed that growth rhythms are fixed and not affected by habitat (cf. *C. compressum*). It is interesting that *H. sericea*, the most prolific *Hakea* species in the South-Western Cape (Neser and Fugler in Stirton, 1978) grows earlier than *H. gibbosa*.

In this investigation three of the four Australian species exhibited growth peaks before the mediterranean species, the reverse of Specht's findings in Australia. Specht observed that '... the efficiency of exotic pine forest can be triggered only by the addition of essential plant nutrients deficient in most Australian soils' (Specht, 1981). There does not appear to be the same constraint on exotic pines or Australian species in the South-Western Cape. The mediterranean regions of Australian heath and South African fynbos are both characterized by the low nutrient status of their soils by comparison with other mediterranean regions (Specht, in press). As such one might expect Australian but not mediterranean exotics to grow in the South-Western Cape without the addition of nutrients.

CONCLUSIONS

From the shoot elongation data described it appears that three of the five non-indigenous species investigated grew earlier than three of the co-habiting indigenous species. This earlier vegetative growth flush is assumed to confer

some competitive advantage which may contribute to the success of these invasive species in both coastal and montane habitats in the South-Western Cape.

ACKNOWLEDGEMENTS

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A NEW *EUPHORBIA* FROM SOUTH-WEST AFRICA

L. C. LEACH*

ABSTRACT

A new dwarf species of *Euphorbia* endemic to a small locality in the "Gariiep Centre", just north of the Orange River is described and is considered to be related to *E. spicata* E. Mey. ex Boiss. and *E. juttae* Dinter.

UITTREKSEL

'N NUWE *EUPHORBIA* VANAF SUID-WES AFRIKA

'n Nuwe dwerg *Euphorbia*-soort, endemies aan 'n klein lokaliteit van die "Gariepsentrum", net noord van die Oranjerivier word beskryf en word as verwant aan *E. spicata* E. Mey. ex Boiss. en *E. juttae* Dinter beskou.

Euphorbia lavrani Leach, sp. nov. verosimiliter ad *E. spicatum* E. Mey. ex Boiss. arcissime affinis sed in diagnose *E. juttae* Dinter melius cognita est utilitius comparata, et hac ramis rigidis, sublignosis, teretibus ad apicem minimis; foliis sessilibus, valde recurvis, plerumque hastatis, atrorubris, marcescentibus; inflorescentia pubescentia, cyathiis minoribus, glandulis saepe 4, ovario tantum partim exserto; capsula minore, stylis pubescentibus, clarissime distinguenda.

Typus: S.W.A., Namuskluft, *Lavranos & Newton 16872* (PRE, holo.; SRGH).

Fruticulus dioecius, succulentus, plerumque aliquam sublignosus, latice debili diluto, e basi ramosus, usque ad 200 mm altus, tantum in terra calcarea crescens. *Rami* ramulique teretes, basi plus minusve 5 mm diam, ad apicem parvulum gradatim decrescentes, obtuse tuberculati, tuberculis decussatis usque ad 1,5 mm prominentibus; in nodis leviter compressi dilatati, in plantis masculis plus minusve recti, in femineis plerumque aliquam decurvi; initio virelli mox grisei. *Folia* sessilia apice tuberculorum disposita, ovata, acuta, saepe aliquam hastata, carinata, supra concava, valde recurva, parce albibubescencia initio virella, mox rufescens, demum fusco-rubrobrunnescentia marcescentia. *Inflorescentia* terminalia, pubescentia, cyathiis saepe numerosis, plerumque in cymis dispositis, pedunculo cymarum ramisque crassis, brevissimis; *bracteae* ovatae acutae, utrinque pubescentes intra pilis longioribus densioribus, rubro-brunneae, longe lateque c. 0,75 mm; *involucrum* olliforme, 1,5-2,0 mm diam, c. 1,0-1,5 mm longum, extus relative dense albi-pubescentia intus versus apicem pilosum,

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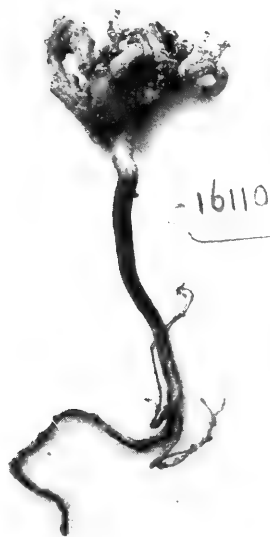


FIG. 1.

Desiccated plant as first received, Oct. 1978. *Euphorbia lavrani*.

glandulis carnosis, patulis, 4-5 (in planta mascula saepissime 4) pallide flavo-virentibus, plerumque plus minusve planis, et lobis fimbriatis pilosis, subquadratis c. 0,4 mm longis latisque, 4-5 (in planta mascula fimbriis singularibus minute clavatis). *Flos masculus* glabrus, bracteolis plumosis, in fasciculis dispositis; *pedicellis* c. 1,75 mm longis, filamentis c. 0,5 mm longis, antherarum thecis pallide viridibus et polline flavo. *Flos femineus* breviter stipitatus, bracteolis plumosis numerosis basin cingentibus; *ovarium* plus minusve ovoideum, c. 1,0 mm longum, 0,75 mm diam; *styli* c. 0,75 mm longi, fere ad basim liberi, late patuli reflexique, apice bifidi stigmatibus late patulis recurvis, virides parce albi-pubescentes. *Capsula* glabra, obtuse 3-lobata, 2,5 mm alta lataque. *Semen* ovoideum basi truncatum, apice subacutum, obscure 4-angulatum, c. 1,75 mm altum, c. 1,1 mm diam., testa grisea vel bubalina, glebulosa, sutura acute sulcata.

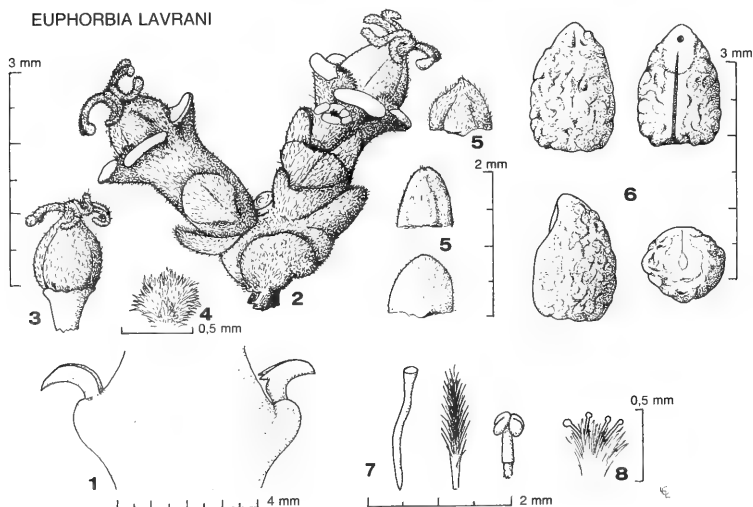


FIG. 2.

Male (16267) and female (16110) plants in cultivation, flowering May 1980. *Euphorbia lavrani*.

Euphorbia lavrani is a much branched and rebranched, dioecious, succulent shrublet up to 200 mm high. Branches and branchlets rigid, terete, ± 5 mm diam. at the base tapering to a small apex, more or less straight and erect to suberect in the male plant, more spreading and somewhat decurved in the female, succulent when young, eventually becoming subwoody with a succulent bark and thin scanty latex; slightly compressed and broadened at the obtusely tumescent nodes with the decussately arranged obtuse tubercles up to 1.5 mm prominent, at first greenish, soon reddening and finally when marcescent becoming dark red-brown. Inflorescence terminal, pubescent, cyathia numerous, clustered (16 seen), usually arranged in cymes, peduncle and cyme branches very short and stout; bracts ovate-acute, ± 0.75 mm long and broad, red-brown, white pubescent, more densely so and with longer hairs on the inside face; in-

volucre tapering obconic truncate, 1,5–2,0 mm diam., 1,0–1,5 mm long with 4–5 spreading fleshy glands, (often $4\frac{1}{2}$), transversely oblong elliptic $\pm 0,75 \times 0,25$ mm, usually more or less flat on the yellow-green upper surface, and 4–5 fimbriate, hairy, subquadrate lobes about 0,4 mm long and wide (in the male plant unique in having minutely clavate fimbria). *Male flowers* glabrous, arranged with plumose bracteoles in separate fascicles with successively developing flowers; *pedicels* $\pm 1,75$ mm long and filaments about 0,5 mm long; anther thecae pale green with yellow pollen. *Female flowers* shortly stipitate, with numerous plumose bracteoles surrounding the base; *ovary* green, \pm ovoid ± 1 mm long, 0,75 mm diam. minutely sparsely pubescent at the apex; *styles* $\pm 0,75$ mm long, free almost to the base, widely spreading reflexed, bifid at the apex with the stigmas widely spreading, recurved. *Capsule* glabrous, pale buff-coloured, obtusely 3-lobed, $\pm 2,5$ mm high and broad. *Seed* obscurely 4-angled, ovoid, truncate at the base, subacute at the apex, $\pm 1,75$ mm high, 1,1 mm thick, with a globulose, grey or buff-coloured testa and an acutely sulcate suture.



1. Node with tubercles and leaves; 2. Terminal cyme; 3. Female flower; 4. Involutral lobe;
5. Bracts of the cyme; 6. Seed, elevation and base views.

All from *Lavranos & Newton 16872*.

7. Male flower with bracteole; 8. Involutral lobe.

All from *Lavranos & Pehlemann 17919*.

S.W.A.—2716 (Witputz): limestone outcrops on Namuskluft (—DD), ♀ cult. SRGH, sub Leach 16110, fl. 1979, fr. 1980, *Lavranos & Newton 16872* (PRE, SRGH); ♂ cult. SRGH sub Leach 16267, fl. 1980, *Lavranos & Pehlemann 17919* (PRE, SRGH).

This new species is restricted to limestone outcrops on Namuskluft near Rosh Pinah (Lavranos), where plants were collected by Lavranos and Newton in 1978. When first received in SRGH plants were very desiccated and in that condition were thought probably to be most nearly related to *E. juttae*.

A female plant was successfully grown in the greenhouse at SRGH and when flowering in 1979 it was seen rather to belong in the affinity of the extremely rare and consequently inadequately known *E. spicata* E. Mey. ex Boiss. Nevertheless it is considered to be more useful to base the diagnosis on comparison with the better known and geographically more closely associated *E. juttae*, with which the new species seems most likely to be confused. In the absence of a male plant no seed was set in 1979 but flowering material was prepared; later in that year a male plant, *Lavranos & Pehlemann 17919*, was collected at the same locality, and seed was obtained in 1980, enabling the description to be completed.

It is with pleasure that this most interesting dwarf species is now named for John Lavranos whose collections in the arid areas of Arabia and the Horn of Africa, as well as in similar parts of south-western Africa need no introduction.

The new species differs widely from *E. juttae* in its subwoody rigid branches tapering to a very small apex, its sessile, strongly recurved, mostly hastate, dark red marcescent leaves and in its pubescent, clustered inflorescence in which the smaller capsule is only partly exerted.

AN ANNOTATED SYSTEMATIC CHECK LIST OF THE SPERMATOPHYTA OF THE SPRINGS RESERVE, UITENHAGE

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ABSTRACT

The vegetation of the Springs Reserve, Uitenhage, is briefly discussed. The 318 species recorded are listed in a systematic check list. Of the 65 Angiospermae families recorded, the Compositae (41 spp.), Liliaceae (32 spp.), Gramineae (20 spp.) and Crassulaceae (18 spp.) are those best represented. The Gymnospermae is represented by one species only.

UITTREKSEL

'N GEANNOTEEERDE SISTEMATIESE KONTROLELYS VAN DIE SPERMATOPHYTA VAN DIE BRONNERESERVAAT, UITENHAGE

Die plantegroei van die Bronnereservaat, Uitenhage, word kortliks bespreek. Die 318 spesies wat aangeteken is, word weergegee in 'n sistematiese kontrolelys. Van die 65 Angiospermae families wat aangeteken is, is die volgende die beste verteenwoordig: Compositae (41 spp.), Liliaceae (32 spp.), Gramineae (20 spp.) en Crassulaceae (18 spp.). Die Gymnospermae word verteenwoordig deur slegs een spesie.

INTRODUCTION

The Springs Reserve is situated 8 kilometres north of the town of Uitenhage, at S 33° 42' and E 25° 27'. The area was proclaimed a nature reserve in 1968 and is administered by the Parks and Amenities Department of the Town Council of Uitenhage. It is approximately 411 ha in extent.

This survey was carried out because a reasonable knowledge of species occurring in a protected area is essential and very little floristic data were available.

METHODS

During the period 1978-1979 the area was visited at regular intervals and specimens were collected in triplicate. The first set is housed in the herbarium of the University of Port Elizabeth, the second set will be placed in the office at the Springs Reserve and the third set (incomplete) was sent to the Botanical Research Unit, Grahamstown, where it was used by the author and the staff of the Unit, for identification purposes.

Plant communities were determined by means of an aerial photograph which was then superimposed on a topographic map of the area. Flowering periods

were recorded as well as presence or absence of species in the different communities. Abundance was estimated on a five-point scale: rare, uncommon, fairly common, common and very common.

RESULTS AND DISCUSSION

Vegetation

Acocks (1975) considers the area to be a karroid type. He classifies it as Valley Bushveld (Veld Type 23) but does not discuss this relationship in the text and only shows it on the map.

During the present survey, two well-defined communities were distinguished: 1. Valley bush and 2. karroid shrub and grass community (Fig. 1).

1. Valley bush

This community is more or less restricted to the low lying areas. It is dense scrub approximately 2–4 metres high, virtually impenetrable with a large number of thorny scramblers.

The most common species are: *Azima tetracantha*, *Capparis sepiaria* var. *citrifolia*, *Euclea undulata*, *Hippobromus pauciflorus*, *Pumbago auriculata*, *Portulacaria afra*, *Ptaeroxylon obliquum*, *Putterlickia pyracantha*, *Sarcostemma viminalis* and *Sideroxylon inerme*.

Two tree *Aloe* species are scattered in the bush—*A. pluridens* and *A. africana*.

The most conspicuous *Euphorbia* is *E. triangularis* occurring in clumps throughout the area.

In the undergrowth *Crassula* spp., *Hypoestis verticillaris* and *Sansevieria hyacinthoides* are abundant.

Towards the higher elevations the bush thins out into bush-clumps.

2. Karroid shrub and grass community

This community occupies the higher elevations outside the valley bushveld. The most important karroid species are: *Becium burchellianum*, *Chrysocoma tenuifolia* and *Felicia filifolia*.

Grasses are mainly represented by *Themeda triandra* and *Cymbopogon marginatus*.

Fynbos influence is seen in the presence of the following species: *Agathosma puberula*, *Bobartia orientalis*, *Disparago ericoides*, *Elytropappus rhinocerotis*, *Erica floribunda*, *Ficinia* spp., *Metalasia muricata*, *Passerina vulgaris* and *Phyllica wilddenowiana*.

On the rocky outcrops the vegetation is sparse showing a succulent character. *Aloe ferox* is concentrated on the western and northern hilltops whereas *A. striata* is more or less confined to Grootkop. The only Gymnosperm found in the survey, *Encephalartos horridus*, is also restricted to the latter area.

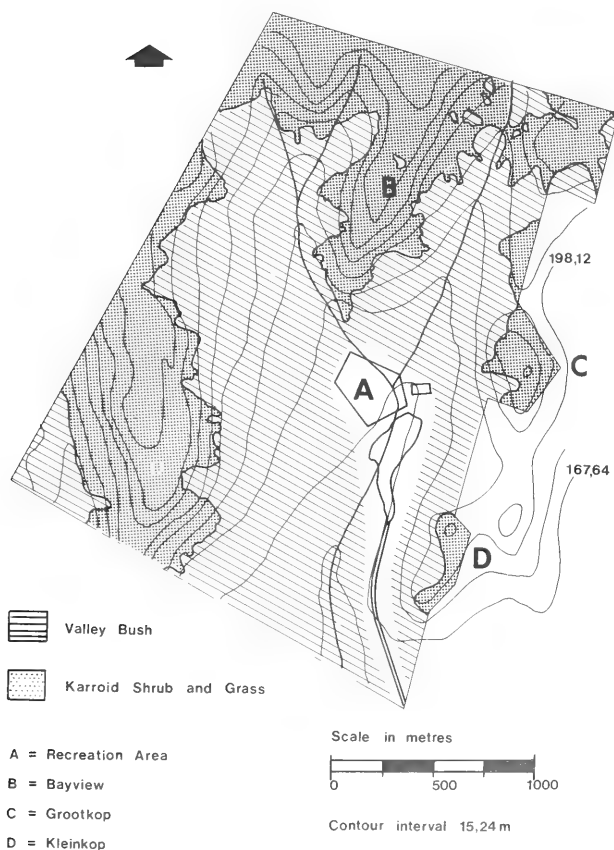


FIG. 1.
Combined Topographic and Vegetation Map of the Springs Reserve, Uitenhage.

Flora

During the survey 65 families, 199 genera and 317 species of angiosperms were listed. An analysis of the families indicates that 10 (15,38 %) are monocotyledons and 55 (84,62 %) are dicotyledons. The first is represented by 86 (27,13 %) and the latter by 231 (72,87 %) species. There are 21 (32,31 %) families whose

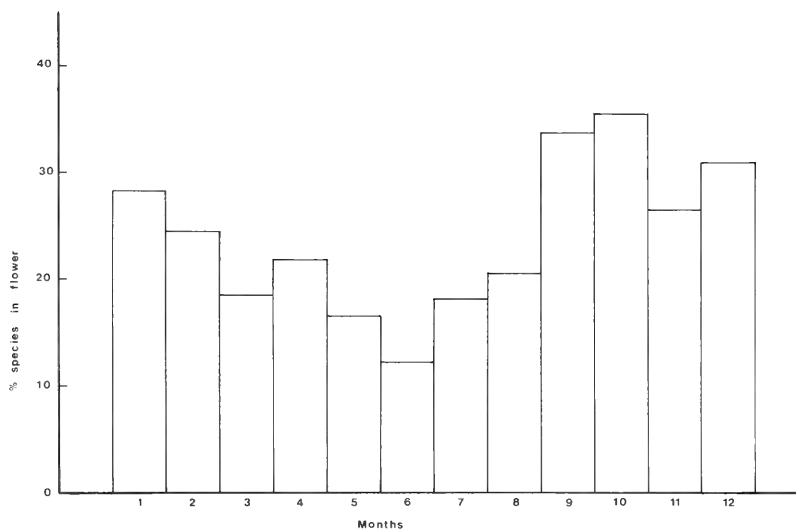


FIG. 2.

Histogram showing the relationship between the percentage of species flowering and the months of the year.

species contribute more than 1,5 % of the total number of species and these are listed in order of numerical importance in Table 1. Twenty-three (35,38 %) families are represented by one species only, eight (12,31 %) by two species, nine (13,85 %) by three species and four (6,15 %) by four species.

Phenology

Flowering periods for 302 species were recorded. An analysis of these is given in Table 2, and indicates that there are signs of a trend for flowering percentage to decrease from January to June and from there onwards to increase reaching a peak in October.

SYSTEMATIC LIST

The systematic list is arranged according to Dyer (1975, 1976). (The numbers refer to the author's collecting number; fl. = flowering period, 1-12 = months of the year.)

ZAMIACEAE

Encephalartos horridus Lehm. 2468, Grootkop, few isolated plants.

TABLE 1.

Synopsis of the families whose species comprise more than 1,5 % of the total number listed in order of numerical importance together with the number of genera.

Family	No. of species	No. of species expressed as a % of total	No. of genera	No. of genera expressed as a % of total
Compositae	41	12,89	24	12,06
Liliaceae	32	10,06	13	6,53
Gramineae	20	6,29	15	7,54
Crassulaceae	18	5,66	4	2,01
Mesembryanthemaceae	12	3,77	9	4,52
Euphorbiaceae	12	3,77	4	2,01
Iridaceae	9	2,83	7	3,52
Celastraceae	9	2,83	4	2,01
Geraniaceae	8	2,52	2	1,01
Campanulaceae	8	2,52	4	2,01
Leguminosae	7	2,20	6	3,02
Anacardiaceae	7	2,20	2	1,01
Asclepiadaceae	7	2,20	7	3,52
Cyperaceae	6	1,89	4	2,01
Amaryllidaceae	6	1,89	5	2,51
Selaginaceae	6	1,89	2	1,01
Acanthaceae	6	1,89	5	2,51
Rubiaceae	6	1,89	3	1,51
Loranthaceae	5	1,57	2	1,01
Ebenaceae	5	1,57	2	1,01
Labiatae	5	1,57	4	2,01

TABLE 2.

Relationship between the percentage of species flowering and the months of the year.

Months	Species	
	Number	% of Total
1	85	28,16
2	74	24,50
3	56	18,54
4	66	21,85
5	50	16,56
6	37	12,25
7	55	18,21
8	62	20,53
9	102	33,77
10	107	35,43
11	80	26,49
12	93	30,79

Total = 302 species

TYPHACEAE

Typha latifolia L. subsp. *capensis* Rohrb. 2469, earth dam, localised.

POACEAE (Gramineae)

Cymbopogon marginatus (Steud.) Stapf ex Burtt Davy 2264, 2328, fl. 8–12, rocky outcrops, fairly common.

Themeda triandra Forsk. 2462, fl. 9–12, western and northern ridges and low lying area between Grootkop and Bayview, common.

Digitaria eriantha Steud. 2463, 2476, fl. 12–1, Bayview and slope above earth dam, fairly common.

Brachiaria serrata (Thunb.) Stapf 2599, fl. 10, northern and western ridges, fairly common.

Panicum deustum Thunb. 2327, fl. 10–12, valley bush in clearings, common.

P. maximum Jacq. 1978, fl. 1, valley bush in clearings, common.

Setaria perennis Hack. 2595, fl. 10, northern ridges, fairly common.

Rhynchelytrum setifolium (Stapf) Chiov. 2325, fl. 10, western ridge and valley bush, in paths, uncommon.

Helictotrichon sp. 2600, fl. 10, valley bush in clearings, uncommon.

Pentaschistis angustifolia (Nees) Stapf 2663, fl. 11, valley bush in paths, common.

P. tortuosa (Trin.) Stapf 2326, 2630, fl. 10, western ridge, common.

Eragrostis capensis (Thunb.) Trin. 2596 fl. 10, western and northern ridges, fairly common.

E. curvula (Schrud.) Nees 2350, fl. 10–11, valley bush, in paths, fairly common.

E. gummiflua Nees 2056, fl. 2, low lying area between Grootkop and Bayview, common.

E. obtusa Munro ex Fical. & Hiern 2461, 2597, fl. 12, valley bush in paths, common.

Cynodon dactylon (L.) Pers. 2662, fl. 10–4, valley bush in clearings, common.

Eustachys mutica (L.) Cufod. 2479, fl. 1, slope above earth dam, fairly common.

Melica racemosa Thunb. 2351, fl. 11, valley bush, in paths, fairly common.

Bromus willdenowii Kunth (= *B. catharticus* Vahl) 2601, fl. 10, valley bush in clearings, common.

Hordeum murinum L. 2665 fl. 12, low lying disturbed areas, common.

CYPERACEAE

Cyperus pulcher Thunb. 2626, fl. 8–10, near earth dam, fairly common.

Ficinia gracilis Schrad. 2628, fl. 10, near earth dam, fairly common.

F. lateralis Kunth 2627, fl. 10, near earth dam, very common.

F. nigrescens (Schrud.) J. Raynal (= *F. bracteata* Boeck.) 2269, fl. 7–8, on rocky outcrops, uncommon.

Scirpus setaceus L. 2624, fl. 10, valley bush in damp areas, common.

Eleocharis limosa Schultz 2625, fl. 10, near north-western boundary in temporary stream, uncommon.

COMMELINACEAE

Commelina africana L. 2415, fl. 10–2, valley bush, along paths, fairly common.

C. benghalensis L. 2004, fl. 12–2, valley bush, along paths, fairly common.

Cyanotis nodiflora Kunth 2123, 2474, fl. 1–3, rocky outcrops above earth dam and Bayview area, uncommon.

LILIACEAE

Bulbine caulescens L. 2362, fl. 1–12, valley bush in clearings, very common.

B. sp. cf. *B. caulescens* L. but bigger, 2562, fl. 9, valley bush, fairly common.

B. latifolia Roem. & Schult. 2316, 2168, fl. 8–4, western ridge and southern low lying open areas, fairly common.

- Chlorophytum capense* (L.) Voss 1996a, fl. 1, near north-eastern boundary on plateau, fairly common.
- Eriospermum* sp. cf. *E. zeyheri* Dyer 2115, 2527, fl. 3, on Bayview and western elevation, fairly common.
- Aloe africana* Mill. 2522, fl. 5–7, scattered in bush, fairly common.
- A. ferox* Mill. 2522, fl. 7–9, western elevation and Bayview, fairly common.
- A. pluridens* Haw. 2569, fl. 7, scattered in bush, fairly common.
- A. striata* Haw. 2221, fl. 7–9, slopes of Grootkop, fairly common.
- Gasteria nigricans* Haw. 2340, fl. 10, on Kleinkop, rare.
- Haworthia xynophylla* Bak. 2169, on rocky outcrops, western elevation, fairly common.
- Agapanthus praecox* Willd. subsp. *orientalis* (Leighton) Leighton 2446, fl. 12–1, Bayview and above earth dam, uncommon.
- Tulbaghia capensis* L. 2704, fl. 4, western ridge, rare.
- T. cepacea* L.f. 2126, fl. 1–4, Bayview area, uncommon.
- Albuca* sp. 2253, fl. 7, on hillside above earth dam, amongst rocks, rare.
- A.* sp. 2296, fl. 9, along footpath from Grootkop to Bayview, rare.
- Scilla* sp. 2482, fl. 1, above earth dam on hilltop, rare.
- Ornithogalum conicum* Jacq. 2660, fl. 11, flowers white, western elevation, fairly common.
- O. dubium* Houtt. 2661, fl. 11, flowers yellow, northern elevation, fairly common.
- O.* cf. *O. longibracteatum* Jacq. 2187, fl. 5, roadside on way to kampong, rare.
- O. virens* Lindl. (= *O. ecklonii* Schlecht.) 2116, fl. 3, Bayview area, rare.
- O.* sp. 2617, 2341, fl. 10, rocky outcrops, uncommon.
- O.* sp. 2355, fl. 11, in path near reservoir, rare.
- Sansevieria hyacinthoides* (L.) Druce 1988, 2443, fl. 12–1, valley bush, in undergrowth, very common.
- Asparagus asparagoides* (L.) Wight 2353, 2545, fl. 10, scattered in valley bush, uncommon.
- A. crassicaladus* Jessop 2085, scattered in valley bush, fairly common.
- A. densiflorus* (Kunth) Jessop 2657, western elevation, uncommon.
- A. racemosus* Willd. 2214, 2261, fl. 5–6, scattered in valley bush, very common.
- A. setaceus* (Kunth) Jessop (= *A. plumosus* Bak.) 2086, scattered in valley bush, fairly common.
- A. striatus* (L.f.) Thunb. 2083, scattered in valley bush, fairly common.
- A. suaveolens* Burch. 2082, 2196, fl. 4, scattered in valley bush, fairly common.
- A. subulatus* Thunb. 2087, 2414, fl. 11–12, scattered in valley bush, fairly common.

AMARYLLIDACEAE

- Haemanthus incarnatus* Burch. 2705, fl. 4–5, western ridge, fairly common.
- Boophane disticha* Herb. not collected, western ridge, rare.
- Brunsvigia gregaria* R. A. Dyer 2525, fl. 2–3, western ridge, uncommon.
- Crinum macowanii* Bak. not collected, fl. 12, Bayview, southern slope amongst rocks, rare.
- Cyrthanthus obliquus* (L.f.) Ait. not collected, fl. 10, Bayview, western slopes, uncommon.
- C. sanguineus* (Lindl.) Walp. not collected, fl. 2–3, southern slopes of Bayview and western elevation, uncommon.

HYPOXIDACEAE

- Hypoxis longifolia* Bak. 2035, fl. 2, Bayview, rare.
- H. sobolifera* Jacq. 2615, fl. 10, western elevation and Bayview area, fairly common.
- H.* sp. 2420, fl. 12, Bayview, rare.
- Spiloxene trifurcillata* (Nel) Fourc. 2206, fl. 5, Bayview, uncommon.

DIOSCOREACEAE

Dioscorea sylvatica (Kunth) Eckl. 2210, 2245, fl. 6, valley bush, uncommon.

IRIDACEAE

Moraea sp. 2549, fl. 9, Bayview, fairly common.

Bobartia orientalis J. B. Gillett 2185, fl. 5, Bayview, western slopes, common.

Aristea pusilla (Thunb.) Ker-Gawl. 2302, fl. 9, low lying open area between Bayview and Grootkop, uncommon.

A. sp. 1983, fl. 1, Bayview, rare.

Tritonia dubia Eckl. ex Klatt 2553, fl. 8–9, low lying areas, common.

T. lineata Ker-Gawl. 2603, fl. 10, northern ridges, fairly common.

Babiana patersoniae L. Bol. 2512, fl. 8–9, northern ridges, uncommon.

Gladiolus liliaceus Houtt. 2640, fl. 10, western ridge, rare.

G. permeabilis Delaroche subsp. *edulis* (Burch. ex Ker) Oberm. 2267, fl. 8, near “eye”, rare.

Freesia corymbosa (Burm. f.) N. E. Br. 2299, fl. 9, Bayview area, western slopes, fairly common.

ORCHIDACEAE

Satyrium maculatum Burch. 2658, fl. 11, western ridge, rare.

Disa sagittalis Swartz 2155, fl. 4, slopes above earth dam, common.

Acrolophia sp. 2422, fl. 12, Bayview, rare.

Eulophia sp. cf. *E. streptopetala* Lindl. 2423, fl. 12, Bayview, rare.

ULMACEAE

Chaetacme aristata Planch. 2430, fl. 12, valley bush, foot of Kleinkop, rare.

MORACEAE

Ficus burtt-davyi Hutch. 2007, Kleinkop, uncommon.

LORANTHACEAE

Moquinella rubra (Spreng. f.) Balle (= *Loranthus elegans* Cham. & Schlecht.) 2134, fl. 4–7, valley bush, uncommon.

Viscum crassulae Eckl. & Zeyh. 2142, fl. 3, valley bush and bush clumps, fairly common.

V. obovatum Harv. 2062, fl. 2, valley bush and bush clumps, fairly common.

V. obscurum Thunb. 2118, fl. 3, valley bush and bush clumps, fairly common.

V. rotundifolium L.f. 1961, 2119, fl. 3, valley bush and bush clumps, fairly common.

SANTALACEAE

Rhoiacarpos capensis (Harv.) A.DC. 2138, fl. 1–12, valley bush and bush clumps, fairly common.

Colpoon compressum Berg. 2067, fl. 2–4, valley bush and bush clumps, fairly common.

Thesium scandens E. Mey. ex DC. 2235, fl. 7, Kleinkop, lower slopes, uncommon.

AIZOACEAE

Galenia sp. 2284, fl. 9, valley bush in open areas, common.

Aizoon glinoides L.f. 2347, fl. 11, valley bush in open areas, common.

MESEMBRYANTHEMACAE

Aptenia cordifolia (L.f.) Schwant. not collected, fl. 4, western ridge, fairly common.

Carpobrotus deliciosus (L. Bol.) L. Bol. 2561, fl. 9, western ridge along road to kampong, common.

- Delosperma ecklonis* (Salm-Dyck) Schwant. 2285, fl. 9–1, valley bush in clearings and rocky outcrops, common.
- D. prasinum* L. Bol. not collected, fl. 2, valley bush, all along paths, common.
- D. truteri* Lavis not collected, fl. 5, western elevation, common.
- Drosanthemum hispidum* (L.) Schwant. 2649, fl. 1, valley bush in clearings, common.
- D. parvifolium* Schwant. 2321, fl. 9–10, valley bush in clearings, common.
- Glottiphyllum longum* (Haw.) N.E.Br. 2667, fl. 11, valley bush in clearing in western part, rare.
- Lampranthus productus* (Haw.) N.E.Br. 2281, fl. 9–2, valley bush in clearings, rocky outcrops, common.
- Mesembryanthemum aitonis* Jacq. 2287, fl. 9, valley bush in clearings, common.
- Platythra haeckeliana* (Berger) N.E. Br. not collected, fl. 1, valley bush in open low lying southern areas, uncommon.
- Ruschia* sp. 2653, fl. 9–1, valley bush, in clearings and rocky outcrops, fairly common.

PORTULACACEAE

- Portulacaria afra* Jacq. 2337, 2448, fl. 10–12, valley bush, common.

CAPPARACEAE

- Capparis sepiaria* L. var. *citrifolia* (Lam.) Toelk. 1976, 2659, fl. 11–12, valley bush, common.
- Maerua afra* (DC.) Pax 1964, 2329, fl. 8–12, valley bush, fairly common.

CRASSULACEAE

- Cotyledon ramosissima* Haw. 2222, fl. 7, Kleinkop and Grootkop, rocky slopes, fairly common.
- C. velutina* Hook. f. var. *beckeri* Schonl. 2011, fl. 7–2, valley bush, common.
- Kalanchoe rotundifolia* Harv. 1781, 2491, fl. 9–5, valley bush in undergrowth, uncommon.
- Crassula capitella* Thunb. subsp. *thyrsiflora* (Thunb.) Toelk. 2289, fl. 9, Bayview, uncommon.
- C. cultrata* L. 2012, fl. 10–2, valley bush in undergrowth, common.
- C. expansa* Dryand. subsp. *expansa* 2226, fl. 7–10, valley bush in undergrowth, common.
- C. mesembryanthoides* (Haw.) Dietr. subsp. *mesembryanthoides* 1780, 2076, fl. 2–5, valley bush in undergrowth, common.
- C. mollis* Thunb. 2458, fl. 12–2, valley bush in undergrowth, common.
- C. muscosa* L. var. *muscosa* 1968, fl. 1, on rocky outcrops, common.
- C. ovata* (Mill.) Druce 2219, fl. 7–8, widespread in valley bush, common.
- C. pellucida* L. subsp. *marginalis* (Dryand.) Toelk. 2254, 2294, fl. 7–12, valley bush in undergrowth, fairly common.
- C. perfoliata* L. var. *falcata* (Wendl.) Toelk. 1997, fl. 1, rocky outcrops, fairly common.
- C. perfoliata* L. var. *miniata* Toelk. 2447, fl. 12–1, rocky outcrops, fairly common.
- C. perforata* Thunb. 2008, 2319, fl. 10–2, valley bush in undergrowth, and rocky outcrops, common.
- C. rupestris* Thunb. subsp. *rupestris* 2218, fl. 7, rocky outcrops, uncommon.
- C. spathulata* Thunb. 2456, fl. 12, valley bush in undergrowth, uncommon.
- C. tetragona* L. 2453, 2318, fl. 10–12, valley bush in undergrowth, common.
- Adromischus rhombifolius* (Haw.) Lem. ex Berger 2000, fl. 12–1, rocky outcrops, common.

MONTINIACEAE

- Montinia caryophyllacea* Thunb. 2433, fl. 10–12, Bayview area, uncommon.

PITTOSPORACEAE

Pittosporum viridiflorum Sims 2191, 2330, fl. 10, bush clumps, fairly common.

LEGUMINOSAE (Fabaceae)

Acacia karroo Hayne 2418, fl. 12–3, scattered in bush, uncommon.

Schottia afra (L.) Thunb. var. *afra* 1979, fl. 1–5, valley bush, common.

S. latifolia Jacq. 2241, 2473, fl. 1–5, valley bush, common.

Aspalathus cinerascens E. Mey. 1977, fl. 1–4, north-eastern plateau, common.

Argyrobolium incanum Eckl. & Zeyh. 2159, fl. 4, western plateau, uncommon.

Indigofera stenophylla Eckl. & Zeyh. 1975, 2037, fl. 12–2, Bayview, uncommon.

Tephrosia capensis (Jacq.) Pers. var. *hirsuta* Harv. 2228, 2039, fl. 7–2, rocky outcrops, common.

GERANIACEAE

Monsonia emarginata (L.f.) L'Hérit. 2040, 2156, fl. 1–4, Bayview, uncommon.

Pelargonium inquinans (L.) L'Hérit. 2147, fl. 4, western plateau, rare.

P. odoratissimum (L.) L'Hérit. 2356, fl. 11–4, valley bush, lower southern slopes, Bayview, uncommon.

P. peltatum (L.) L'Hérit. 1990, fl. 8–1, valley bush, common.

P. radens H.E. Moore 2202, 2249, fl. 1–7, rocky slopes, fairly common.

P. reniforme Curt. 2081, 2184, fl. 2–5, widespread, common.

P. sp. 2162, fl. 4, Bayview area, uncommon.

P. sp. 2514, fl. 10, western ridge, fairly common.

OXALIDACEAE

Oxalis smithiana Eckl. & Zeyh. 2248, fl. 9, grassy slopes above earth dam, uncommon.

O. stellata Eckl. & Zeyh. 2144, fl. 4, low lying open areas in valley bush, common.

O. sp. 2548, fl. 9, Bayview, eastern slopes, fairly common.

ZYGOPHYLLACEAE

Zygophyllum uitenhagense Sond. 2342, fl. 10, Kleinkop, uncommon.

RUTACEAE

Zanthoxylum capense (Thunb.) Harv. (= *Fagara capensis* Thunb.) 2442, fl. 11–5, valley bush, uncommon.

Agathosma puberula Fourc. 2199, 2520, fl. 3–10, western elevation and Bayview, fairly common.

Clausena anisata (Willd.) Hook.f. ex Benth. 2609, fl. 10, bush clumps, uncommon.

PTAEROXYLACEAE

Ptaeroxylon obliquum (Thunb.) Radlk. 2335, fl. 9–10, valley bush, fairly common.

POLYGALACEAE

Polygala ericaefolia Harv. 2551, fl. 9, Bayview, western slopes, fairly common.

P. myrtifolia L. 2244, fl. 7–2, Kleinkop and Grootkop, common.

P. virgata Thunb. var. *genistoides* Harv. 2470, fl. 9–1, valley bush, fairly common.

EUPHORBIAEAE

Phyllanthus verrucosus Thunb. 2556, fl. 9–12, valley bush, common.

Jatropha capensis Sond. 2053, 2237, fl. 1–12, valley bush, common.

Clusia affinis Sond. 2535, fl. 7–9, valley bush, common.

Euphorbia clava Jacq. 2113, 2290, fl. 3, 7, 9, rocky outcrops, fairly common.

E. globosa (Haw.) Sims 2564, fl. 9, western ridge, rare.

- Euphorbia ledienii* Berger 2293, 2322, fl. 9–10, rocky outcrops and valley bush, in undergrowth, common.
E. mammillaris L. 2575, fl. 9, valley bush, in undergrowth, uncommon.
E. mauritanica L. 2215, 2303, fl. 7–9, valley bush, common.
E. polygona Haw. 2069, 2217, fl. 7, rocky outcrops, common.
E. rhombifolia Boiss. 2434, fl. 12, Bayview, fairly common.
E. stellata Willd. 2523, fl. 10, western elevation and Bayview, fairly common.
E. triangularis Desf. 2323, fl. 10, valley bush, in clumps, fairly common.

ANACARDIACEAE

- Loxostylis alata* Spreng. ex Reichb. 2541, fl. 12, rocky outcrops, fairly common.
Rhus excisa Thunb. 2139, fl. 4, valley bush and bush clumps, fairly common.
R. glauca Thunb. 2242, 2292, fl. 7, valley bush and bush clumps, common.
R. incisa L.f. var. *obovata* (Sond.) Schönl. 2537, fl. 9, valley bush and bush clumps, common.
R. longispina Eckl. & Zeyh. 2313, 2467, fl. 10–1, valley bush and bush clumps, common.
R. lucida L. 2620, 2674, fl. 4, valley bush and bush clumps, fairly common.
R. refracta Eckl. & Zeyh. 2619, valley bush and bush clumps, uncommon.

CELASTRACEAE

- Maytenus capitata* (E. Mey. ex Sond.) Marais 2080, fl. 9, valley bush and bush clumps, fairly common.
M. heterophylla (Eckl. & Zeyh.) N. Robson 2054, 2436, fl. 9–12, bush clumps, common.
M. polyacantha (Sond.) Marais 1806, fl. 7, valley bush, fairly common.
M. undata (Thunb.) Blakelock 2673, fl. 11, valley bush, fairly common.
Putterlickia pyracantha (L.) Szyszyl. 1807, 2441, fl. 10–11, valley bush, very common.
Pterocelastrus tricuspidatus (Lam.) Sond. 2332, fl. 10, bush clumps, fairly common.
Cassine aethiopica Thunb. 1960, 2633, fl. 9, valley bush and bush clumps, fairly common.
C. crocea (Thunb.) Kuntze 1958, 2236, valley bush and bush clumps, fairly common.
C. reticulata (Eckl. & Zeyh.) Codd 2052, 2291, valley bush and bush clumps, fairly common.

ICACINACEAE

- Apodytes dimidiata* E. Mey. ex Arn. 2051, 2167, fl. 12–2, bush clumps, fairly common.

SAPINDACEAE

- Allophylus decipiens* (Sond.) Radlk. 173, fl. 12–1, foot of Grootkop, uncommon.
Pappea capensis Eckl. & Zeyh. 2557, fl. 9, valley bush, uncommon.
Hippobromus pauciflorus (L.f.) Radlk. 2333, fl. 10, valley bush, fairly common.

RHAMNACEAE

- Scutia myrtina* (Burm. f.) Kurz 2431, 2623, fl. 12–1, valley bush, common.
Phyllica wilddeniowiana Eckl. & Zeyh. 2043, 2452, fl. 1–12, Bayview, uncommon.

VITACEAE

- Rhoicissus digitata* (L.f.) Gilg & Brandt 1959, fl. 1–4, valley bush, very common.
Rhoicissus tridentata (L.f.) Wild & Drummond 2065, 2151, fl. 1–4, valley bush, very common.

TILIACEAE

- Grewia occidentalis* L. 2360, fl. 10–1, valley bush, common.

MALVACEAE

- Abutilon sonneratianum* (L.) Sweet 2250, fl. 7–9, along paths in valley bush, common.
Hibiscus trionum L. 2129, fl. 4, southern slope of Bayview, rare.

STERCULIACEAE

- Melhanian didyma* Eckl. & Zeyh. 2150, western elevation, uncommon.
Hermannia althaeoides Link 2352, fl. 9–12, Bayview and along paths in valley bush, fairly common.
H. velutina DC. 2256, fl. 8, near earth dam, uncommon.

OCHNACEAE

- Ochna arborea* Burch. ex DC. var. *arborea* 1093, 1416, fl. 6–10, valley bush and bush clumps, fairly common.
O. serrulata (Hochst.) Walp. 2547, fl. 9, valley bush and bush clumps, fairly common.

FLACOURTIACEAE

- Scolopia zeyheri* (Nees) Harv. 2559, 2587, fl. 9, western elevation, uncommon.

THYMELAEACEAE

- Gnidia capitata* L.f. 2046, 2594, fl. 2, Bayview, uncommon.
G. styphelioides Meisn. 2592, fl. 10, western slopes of Bayview, uncommon.
Struthiola parviflora Bartl. 2593, fl. 10, western slopes of Bayview, uncommon.
Passerina vulgaris (Meisn.) Thoday 2554, fl. 9, rocky outcrops, very common.

ARALIACEAE

- Cussonia spicata* Thunb. 2146, fl. 6, bush clumps, fairly common.

UMBELLIFERAE (Apiaceae)

- Glia gummifera* (L.) Sond. 2058, fl. 2, Bayview, uncommon.

ERICACEAE

- Erica floribunda* Lodd. 2197, fl. 5, in kloof near north-eastern boundary, in damp habitat, uncommon.

PLUMBAGINACEAE

- Plumbago auriculata* Lam. 1992, fl. 1–12, valley bush, common.

SAPOTACEAE

- Sideroxylon inerme* L. 2558, fl. 11–1, valley bush, fairly common.

EBENACEAE

- Euclea polyandra* E. Mey. ex Hiern 2182, fl. 5, Bayview, fairly common.
E. schimperi (A.D.C.) Dandy var. *daphnoides* (Hiern) De Wint. 1636, 1771, fl. 4, rocky slopes, fairly common.
E. undulata Thunb. 2047, 2135, fl. 1–2, valley bush, fairly common.
Diospyros dichrophylla (Gand.) De Wint. 1962, fl. 12, valley bush, fairly common.
D. scabrida (Harv. ex Hiern) De Wint. var. *cordata* (E. Mey. ex A.D.C.) De Wint. 2121, 2263, fl. 8–10, rocky slopes, fairly common.

OLEACEAE

- Olea africana* Mill. 2063, 2435, fl. 12, valley bush, fairly common.
Jasminum angulare Vahl 1972, fl. 11, valley bush and bush clumps, fairly common.
J. multipartitum Hochst. 1971, 2002, fl. 10, valley bush and bush clumps, common.

SALVADORACEAE

Azima tetraacantha Lam. 2536, fl. 9–6, valley bush, common.

LOGANIACEAE

Nuxia floribunda Benth. 2560, fl. 9, stream near north-western boundary, rare.

Buddleja saligna Willd. 2361, fl. 11–1, valley bush, fairly common.

APOCYNACEAE

Acokanthera oppositifolia (Lam.) Codd 2334, fl. 9, valley bush, uncommon.

Carissa haematocarpa (Eckl.) A.DC. 2437, fl. 12, valley bush, common.

Pachypodium bispinosum (L.f.) A.DC. 2295, 2419, fl. 2, 9, 12, on ridges, common.

P. succulentum (L.f.) A.DC. 2676, fl. 11, valley bush, uncommon.

ASCLEPIADACEAE

Cynanchum tetrapterum (Trucz.) R.A. Dyer 2188, fl. 2–7, valley bush, common.

Sarcostemma viminalis (L.) R. Br. 2006, 2220, fl. 1–12, valley bush, common.

Secamone frutescens (E. Mey.) Decne. 2224, 2455, fl. 12–1, valley bush, common.

Ceropegia ampliata E. Mey. 2048, fl. 2, Kleinkop, rare.

Stapelia grandiflora Mass. not collected, valley bush, rare.

Huernia primulina N.E. Br. 2122, fl. 3, western slope of Bayview, uncommon.

Fockea edulis (Thunb.) K. Schum. 2492, fl. 2, valley bush, fairly common.

CONVOLVULACEAE

Ipomoea ficifolia Lindl. 1987, fl. 1–4, foot of Kleinkop, uncommon.

BORAGINACEAE

Ehretia rigida (Thunb.) Druce 1981, fl. 8–1, valley bush, fairly common.

VERBENACEAE

Lantana salvifolia Jacq. 1966, 2186, fl. 1, 5, 9, Bayview, uncommon.

Chascanum dehiscens (L.f.) Moldenke 2152, fl. 4, western elevation, fairly common.

LABIATAE (Lamiaceae)

Leonotis leonitis R. Br. 2127, fl. 1–12, western elevation and Bayview, uncommon.

Salvia triangularis Thunb. 2607, fl. 10, valley bush in underground, common.

Plectranthus hirtus Benth. 2647, fl. 6, valley bush in undergrowth, very common.

P. spicatus E. Mey. 2057, fl. 2, Bayview, uncommon.

Becium burchellianum N.E. Br. 1984, fl. 9–2, western and northern elevations, common.

SOLANACEAE

Solanum rubetorum Dun. 2516, fl. 8, near earth dam, uncommon.

SCROPHULARIACEAE

Sutera pinnatifida (Benth.) Kuntze 2198, fl. 1–12, western and northern elevations, common.

S. polyantha Kuntze 2153, fl. 1–12, western elevation, common.

Alectra capensis Thunb. 2417, 2515, fl. 12, 8, Bayview and western elevation, uncommon.

SELAGINACEAE

Selago corymbosa L. 2465, fl. 1–12, Bayview, fairly common.

S. dregei Rolfe 2466, 2634, fl. 1–12, Bayview, uncommon.

- Selago forbesii* Rolfe 2349, fl. 1–12, Bayview, fairly common.
Walafrida decipiens (E. Mey.) Rolfe 2204, fl. 1–12, Bayview, fairly common.
W. geniculata Rolfe 1991, fl. 1–12, Bayview, fairly common.
W. nitida E. Mey. 2203, fl. 1–12, Bayview, very common.

BIGNONLACEAE

- Tecomaria capensis* (Thunb.) Spach 2542, fl. 9, western ridge, rare.

ACANTHACEAE

- Thunbergia capensis* Retz. 1989, 2477, fl. 1, western plateau, rare.
Barleria obtusa Nees not collected, Bayview, rare.
B. pungens L.f. 2031, fl. 2, Bayview, rare.
Blepharis procumbens (L.f.) Pers. 2606, fl. 9–12, Bayview, uncommon.
Hypoestis verticillaris (L.f.) R. Br. 2544, fl. 1–12, valley bush, in undergrowth, common.
Justicia capensis Thunb. 2343, fl. 8–10, Grootkop and Kleinkop, uncommon.

RUBLACEAE

- Xeromphis rudis* (E. Mey. ex Harv.) Codd 2555, fl. 9, rocky outcrops, fairly common.
Canthium inerme (L.f.) Kuntze 2538, fl. 9, bush clumps, fairly common.
C. mundianum Cham. & Schlecht. 2472, fl. 9, rocky outcrops, fairly common.
C. obovatum Klotzsch 1956, 2164, fl. 1–4, valley bush, fairly common.
C. spinosum (Klotzsch) Kuntze 2570, fl. 9–10, bush clumps, fairly common.
Pavetta capensis (Houtt.) Brem. 2416, fl. 12–1, valley bush and bush clumps, uncommon.

CUCURBITACEAE

- Kedrostis nana* (Lam.) Cogn. var. *zeyheri* (Schr.) A. Meeuse 2262, fl. 8, valley bush, uncommon.

CAMPANULACEAE

- Wahlenbergia capillacea* A. DC. 2033, fl. 2, Bayview, uncommon.
W. undulata (L.f.) A. DC. 2133, 2655, fl. 4, valley bush, along path in western part of reserve, rare.
Lightfootia divaricata Buek 2637, fl. 10, western ridge, common.
L. rubens Buek 2032, fl. 2–7, Bayview, uncommon.

LOBELIACEAE

- Cyphia* sp. cf. *C. linarioides* Presl 2157, fl. 3, Bayview, uncommon.
C. undulata Eckl. 2124, fl. 4, western elevation, uncommon.
Lobelia sp. 2638, fl. 10, slopes above earth dam in damp places, common.
Monopsis scabra (Thunb.) Urb. 2132, fl. 1–12, near earth dam, fairly common.

COMPOSITAE (Asteraceae)

- Vernonia capensis* (Houtt.) Druce 2421, fl. 12, Bayview, uncommon.
Pteronia incana (Burm.) DC 2308, fl. 9, Bayview and western elevation, common.
Felicia fascicularis DC. 2357, fl. 9–11, valley bush in clearings, common.
F. filifolia (Vent.) Burt Davy 2513, fl. 8–10, western and north-eastern elevations, common.
Microglossa mespilifolia (Less.) C. B. Robinson 2268, fl. 8, lower southern slopes of Bayview, uncommon.
Chrysocoma tenuifolia Berg. 2045, fl. 1–12, Bayview area and western elevation, common.
Brachylaena elliptica (Thunb.) DC. 2141, 2190, fl. 12–5, northern and western ridges, fairly common.

- Brachylaena ilicifolia* (Lam.) Phill. & Schweick. 2445, fl. 12, northern side of reserve, uncommon.
- Tarchonanthus camphoratus* L. 1957, fl. 1–3, Bayview and western elevation, fairly common.
- Helichrysum cymosum* (L.) D. Don 2451, 2475, fl. 9–1, Bayview and above earth dam, fairly common.
- H. rosum* (Berg.) Less. 2449, fl. 9–1, above earth dam, fairly common.
- H. teretifolium* (L.) D. Don 2610, fl. 10, above earth dam, fairly common.
- H. sp.* 2611, fl. 10, valley bush, Bayview, rare.
- Disparago ericoides* Gaertn. 2517, fl. 8, western elevation, fairly common.
- Elytropappus rhinocerotis* (L.f.) Less. 2519, fl. 8, Bayview and western elevation, common.
- Metalasia muricata* (L.) D. Don 2518, fl. 8, western elevation, fairly common.
- Relbunium genistaefolia* (L.) L'Hérit. 2257, fl. 8–9, Bayview and western elevation, very common.
- Athanasia dentata* L. 2664, fl. 11, uncommon.
- Cotula sp. cf. C. anthemoides* L. 2359, fl. 11, low lying areas where bush has been cleared, common.
- Pentzia globifera* (Thunb.) Hutch. 2605, fl. 10, in valley bush in clearing, uncommon.
- Cineraria lobata* L'Hérit. 1985, fl. 3–10, valley bush in paths, fairly common.
- Senecio acaulis* (L.f.) Sch. Bip. 2529, 2567, fl. 4–10, western elevation, fairly common.
- S. ilicifolius* Thunb. 2358, fl. 11, low lying areas where bush has been cleared, uncommon.
- S. inaequidens* DC. 2201, 2232, fl. 5–7, valley bush in paths, fairly common.
- S. junceus* Harv. 2038, fl. 2, on rocky outcrops, common.
- S. longifolius* L. 2231, fl. 7–12, on rocky outcrops, common.
- S. macroglossus* DC. 2137, 2191, fl. 4–5, valley bush, uncommon.
- S. mikanioides* Otto ex Harv. 2243, fl. 7, valley bush, uncommon.
- S. pyramidatus* DC. 2213, 2306, fl. 7–9, valley bush in undergrowth, fairly common.
- S. radicans* (L.f.) Sch. Bip. 2565, fl. 10–11, valley bush in undergrowth, common.
- S. scaposus* DC. 2071, 2450, fl. 1–2, rocky outcrops, fairly common.
- S. vitalis* N.E. Br. 2223, 2568, fl. 2, rocky outcrops, common.
- Kleinia repens* (L.) Haw. 2588, fl. 4–10, western elevation, fairly common.
- Euryops algoensis* DC. 2130, fl. 4, valley bush in clearings, uncommon.
- E. euryopoides* (DC.) B. Nordenstam 2005, fl. 4–9, rocky koppies, common.
- Osteospermum imbricatum* L. 2608, fl. 9–10, western and northern elevations, uncommon.
- Chrysanthemoides monilifera* (L.) Norl. 2247, fl. 4–9, western elevation, uncommon.
- Ursinia nana* DC. 2604, fl. 10, in valley bush in clearing, uncommon.
- Venidium decurrens* Less. 2136, 2195, fl. 4–5, Bayview, fairly common.
- Haplocarpha lyrata* Harv. 2200, fl. 1–12, Bayview, fairly common.
- Gazania linearis* (Thunb.) Druce 2251, fl. 8–1, near earth dam, fairly common.

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NOTES ON *HAEMANTHUS*: TWO NEW SPECIES FROM THE WESTERN CAPE

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ABSTRACT

The Namaqualand species known previously in South African herbaria as *Haemanthus undulatus* Herbert, a name which is antedated by *Haemanthus undulatus* (L.) Thunb., is described *de novo* as *Haemanthus crispus* Snijman. *Haemanthus barkeriae* Snijman, a new species from the Western Cape Province is also described. Both species are illustrated.

UITTREKSEL

NOTAS OOR *HAEMANTHUS*: TWEE NUWE SPESIES UIT DIE WESTELIKE KAAPPROVINSIE

Die Namakwalandse spesie wat voorheen in Suid-Afrikaanse herbaria benoem is as *Haemanthus undulatus* Herbert, voorafgegaan deur die ouer naam *Haemanthus undulatus* (L.) Thunb., word *de novo* beskryf as *Haemanthus crispus* Snijman. *Haemanthus barkeriae* Snijman, 'n nuwe spesie uit die Westelike Kaapprovinsie, word ook beskryf. Albei spesies word geïllustreer.

Haemanthus crispus Snijman, sp. nov.

Haemanthus crispus Snijman species nova; foliis angustis (7-33 mm latis) loratis canaliculatis sinuatis, et inflorescentiis 4-6 valvis spathis late obtrullatis rubris erectis aequantibus flores, distinguitur.

Bulbus obclavatus vel globosus, solitarius vel caespitosus, ad 60 mm diam., in sectione transversali rotundus vel mediane leviter compressus; tunicae aequaliter marcescentes, papyracentes, et atrofuscentes; tunicae interiores carnosae, albae. *Folia* dua, interdum unica vel tertia, hysternantha, suberecta vel recurvata; lamina lorata. 100-200(-350) mm longa, 7-20(-33 mm) lata, canaliculata, viridis vel glauca, pilis brevis rigidis tenuiter vel dense vestita; pagina abaxialis marronina et atroviridi maculata, basin versus aliquam costata; margina per totam longitudinem sinuata vel undulata, vel tantum basin versus, raro plana, plerumque rubidis limitata. *Pedunculus* ad 150 mm longus, 6-12 mm latus et 4-5 mm crassus, rubescens, immaculatus vel atrorubro punctatus, glaber. *Umbella* obovata ad obconica, 15-40 mm lata supra. *Valvae spathaceae* 4-5(-6), erectae, aeqans flores plus minusve, late obtrullatae ad spathulatae, 22-40 mm longae, 13-35 mm latae supramediae, rubellae, ceraceae et carnosae; apices

plerumque obtusi et mucronati. *Flores* 6–25, compacti, rubri, basi et apice albescentes. *Pedicilli* 1–4(–7) mm longi, rubelli. *Perianthium* 15–26 mm longum; tubus 2–9 mm longus, sexgibbosus superne; segmenta erecta, lineares ad anguste spathulata, 12–20 mm longa, 0.75–2 mm lata; apices obtusi, ampliati. *Filamenta* ad 10 mm exserta, albida ad rubella. *Antherae* 1–2 mm longae ubi apertae, luteae. *Ovarium* subglobosum, 2–4 diam., viride vel erubescens. *Stylus* stamina leviter excedens. *Baccae* sphaericae, 13–20 mm diam., roseae et pulposae ubi maturae, arcte fasciculatae. *Semina* 1–4, globosa ad 10 mm diam., atrophyrea.

Type: South Africa, Namaqualand, 61 km north of Vanrhynsdorp towards Nuwerus, 28/3/1981, *Snijman 410* (NBG, holotype; K, MO, PRE, S, isotypes). Fig. 1.

Bulb obclavate to globose, solitary or clumped, up to 60 mm diam., round in cross section or slightly compressed in the median plane; tunics dying down evenly forming a dark brown papery covering; inner tunics fleshy and whitish. *Leaves* 2, occasionally 1 or 3, appearing shortly after the inflorescence, suberect or recurved; blade lorate, 100–200(–350) mm long, 7–20(–33) mm wide, canaliculate, green or glaucous, sparsely to densely hirsute with short, stiff hairs; abaxial surface with dark green and maroon blotches, somewhat ribbed towards the base; margins sinuate to undulate throughout, or towards the base only, rarely entirely flattened, usually outlined with red. *Peduncle* up to 150 mm long, 6–12 mm wide and 4–5 mm thick, pure red or occasionally with dark red mottling, glabrous. *Umbel* obovate to obconical, 15–40 mm wide above. *Spathe valves* 4–5(–6), erect and more or less equalling the flowers, broadly obtrullate to spathulate, 22–40 mm long, 13–35 mm broad above the middle, coral to scarlet, waxy and fleshy; tips mostly obtuse and mucronate. *Flowers* 6–25, compact, coral to scarlet, whitish at the base and tips. *Pedicels* 1–4(–7) mm long, pale scarlet. *Perianth* 15–26 mm long; tube 2–9 mm long, with six gibbosities above; segments erect, linear to narrowly spathulate, 12–20 mm long, 0.75–2 mm wide; tips obtuse, swollen. *Filaments* exserted by up to 10 mm, whitish to pale scarlet. *Anthers* 1–2 mm long when open, yellow. *Ovary* subglobose, 2–4 mm diam., green to rosy. *Style* slightly exceeding the stamens. *Berries* spherical, 13–20 mm diam., pale pink and pulpy when ripe, tightly clustered together. *Seeds* 1–4, globose up to 10 mm diam., dark reddish-brown.

Flowering time: March–April (–May); usually up to a month earlier in cultivation.

Leafing period: leaves emerge from May and die back by October.

Distribution: the species is found in abundance throughout Namaqualand. It grows in a variety of habitats, ranging from the flat sandy coastal plain in the

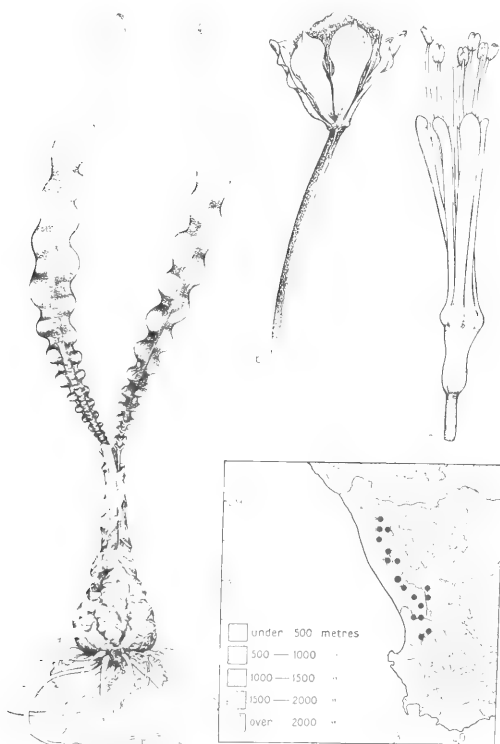


FIG. 1.

Morphology and distribution of *Haemanthus crispus* Snijman. a, bulb and leaves approx. $\times \frac{1}{2}$; b, inflorescence $\times \frac{1}{2}$; c, flower $\times 2$.

west through to sandstone outcrops along the first escarpment in the east, along the banks of the Olifants River in the south to amongst granite boulders near Steinkopf in the north (Fig. 1).

The features of *Haemanthus crispus* which make it distinctive, are its narrow, lorate sinuate and canaliculate leaves which are nearly always covered with very short stiff hairs. The inflorescence typically has few spathe valves, 4–6 in number. These are erect, scarlet, usually broadly obtrullate and more or less equal in length to the flowers. The flowers have short pedicels, usually less than 5 mm long and the perianth tube is distinctly six gibbose above.

In South African herbaria this species has previously been referred to as *Haementhus undulatus* Herbert. The use of Herbert's name, however, is invalidated by the prior existence of *H. undulatus* (L.) Thunb., now a synonym of *Nerine undulata* (L.) Thunb. An examination of the incomplete and very damaged remains of Herbert's type of *H. undulatus* (a Masson collection in the British Museum) left the author in some doubt as to its true identity. Consequently, it was deemed necessary to select a new type and to describe the species *de novo*.

CAPE—2917 (Springbok): Steinkopf (–BC), *Stayner* sub. KG 347/69 (NBG); Niegramoep (–DA), *Wikner s.n.* (SAM 63136); farm Driekoppe, south of Springbok (–DB), *Snijman 421* (K, NBG, PRE); O'okiep, *Giffen* sub *Marloth 11955* (PRE); Concordia, *Krapohl* sub *Marloth 5788* (PRE); Sannagass (–DC), *van Jaarsveld 5327* (NBG).

—3017 (Hondeklipbaai): 8 km west of national road N7 towards Grootvlei (–BB), *Snijman 414* (MO, NBG, PRE); 4 km west of farm Outuin, ascending Kamiesberg Pass, *Snijman 423* (NBG, PRE); Brakdam, 12 km north of Garies (–BD), *Bayer 349* (NBG); Darters Grave, 22 miles north of Garies, *Booyesen 12* (NBG), *Middlemost 2157* (NBG), *Snijman 412* (PRE).

—3018 (Kamiesberg): south-west slopes of Kamiesberg, along Studers Pass (–AC), *Snijman 426* (NBG, PRE); about 4.5 km south of Welkom (–AC/CA), *van Berkel 117* (NBG, PRE); 14.5 km north of Bitterfontein towards Garies (–CC), *Snijman 427* (K, NBG, PRE).

—3118 (Vanhynsdorp): 61 km north of Vanhynsdorp towards Nuwerus (–AB), *Snijman 410* (K, MO, NBG, PRE, S); 2 km north of Bitterfontein towards Garies, *van Berkel 119* (K, NBG, PRE); farm Steenkampskraal (–BC), *Hall 4113* (NBG); 2 km south of gate to Sandkraal farmhouse (–DB), *Snijman 429* (NBG); Klaver (–DC), *Compton* sub NBG 308/22 (BOL); 2.6 miles west of N7 road from Trawal towards Skurfkop, *Hardick* sub NBG 889/71 (NBG, PRE); top of Nardouws Pass ascending from near Trawal, *Snijman 289* (NBG); north of Bulshoek Barrage (–DD), *Barker 7304* (NBG).

—3119 (Calvinia): about 11 km north-east of Grasberg towards Theunisdrift (–AA), *Snijman 140* (NBG); foot of Vanhyns Pass (–AC), *Snijman 142* (NBG).

—3218 (Clanwilliam): farm Alpha at Algeria turnoff (–BD), *Fisher 13* (NBG).

—3219 (Wuppertal): Pakhuis (–AA), *Salter 7523* (NBG).

***Haemanthus barkerae* Snijman, sp. nov.**

Haemanthus barkerae Snijman species nova; inflorescentii roseis 4–5 valvis spathis patentibus. Species foliis angustis (7–25 mm latis) loratis pilis brevis, et canaliculatis in dimidio inferiore, et marginibus parallelis fere, a congeneribus diversa.

Bulbus globosus vel obclavatus, solitarius, ad 45 mm diam., in sectione transversali rotunde plus minusve; tunicae exteriores oblique marcescentes, papyraceae et atrofuscae; tunicae interiores carnosae, albae. *Folia* dua interdum unica, hysteroantha, recurvata vel interdum suberecta, anguste lorata, 90–260(–340) mm longa, 7–20(–25) mm lata, marginibus parallelis fere, in dimidio inferiore canaliculata aliquantum; pagina viridis vel atroviridis, pilis brevis rigidis subtus vel interdum utrinque, interdum glabrata; pagina abaxialis rubida et atroviridi extense fasciata; margina rubella. *Pedunculus* gracilis ad 140 mm longus, 4–7 mm latus et 3–4 mm crassus, roseus, interdum leviter marmoratus, glaber vel interdum pilis brevis. *Umbella* obconica, patens, 35–60 mm lata. *Valvae spathaceae* 4(–5), patentes, floribus longiorae vel breviorae, oblongae lanceolatae, (20–)25–50 mm longae, 4–16 mm latae ad medium, roseae, ubi novellae lucentes; apices acuti. *Flores* 7–30, laxi, roseoli, apice albescentes. *Pedicilli* (4–)7–18 mm longi, roseoli. *Perianthium* 13–18 mm longum; tubus 1.5–3 mm longus, laevis, anguste campanulatus; segmenta patentia aliquantum lineares ad anguste lanceolata, 11–16 mm longa, 1.5–2 mm lata; apices obtusi vel subacuti. *Filamenta* ad 8 mm exserta, roseola ad albida. *Antherae* 1.5–2 mm longae ubi apertae, luteae. *Ovarium* subglobosum, 2–3 mm diam., viride vel erubescens. *Stylus* stamina leviter excedens.

Type: South Africa, Cape Province, 63.5 km from Calvinia on the road towards Loeriesfontein, fl. NBG 14/4/1980, *Snijman 132* (NBG, holotype; PRE, isotype). (Fig. 2.).

Bulb globose to obclavate, solitary, up to 45 mm diam., more or less circular in cross section; outer tunics dying down slightly obliquely, usually forming a dark brown papery covering; inner tunics fleshy and whitish. *Leaves* 2, occasionally 1, appearing shortly after the inflorescence, recurved or occasionally sub-erect, narrowly lorate, 90–260(–340) mm long, 7–20(–25) mm wide, with almost parallel sides, somewhat canaliculate in the lower half; blade dull or light green, with short stiff hairs covering the abaxial surface, or occasionally both surfaces, sometimes glabrous: abaxial surface with extensive red and dark green barring; margin reddish. *Peduncle* slender, up to 140 mm long, 4–7 mm by 3–4 mm wide, reddish-pink, sometimes faintly marbled, glabrous or occasionally sparsely covered with short hairs. *Umbel* obconical, spreading, 35–60 mm across. *Spathe valves* 4(–5), spreading almost to a horizontal position, shorter or longer than the flowers, oblong lanceolate, (20–)25–50 mm long, 4–16 mm broad near the middle, rose to magenta-rose, glistening and fleshy when fresh; tips acute. *Flowers* 7–30, lax, rose-pink with white tips. *Pedicels* (4–)7–18 mm long, pinkish. *Perianth* 13–18 mm long; tube 1.5–3 mm long, smooth, narrowly campanulate; segments somewhat spreading, linear to narrowly lanceolate, 11–16 mm long, 1.5–2 mm wide; tips obtuse or subacute. *Filaments* exserted by up

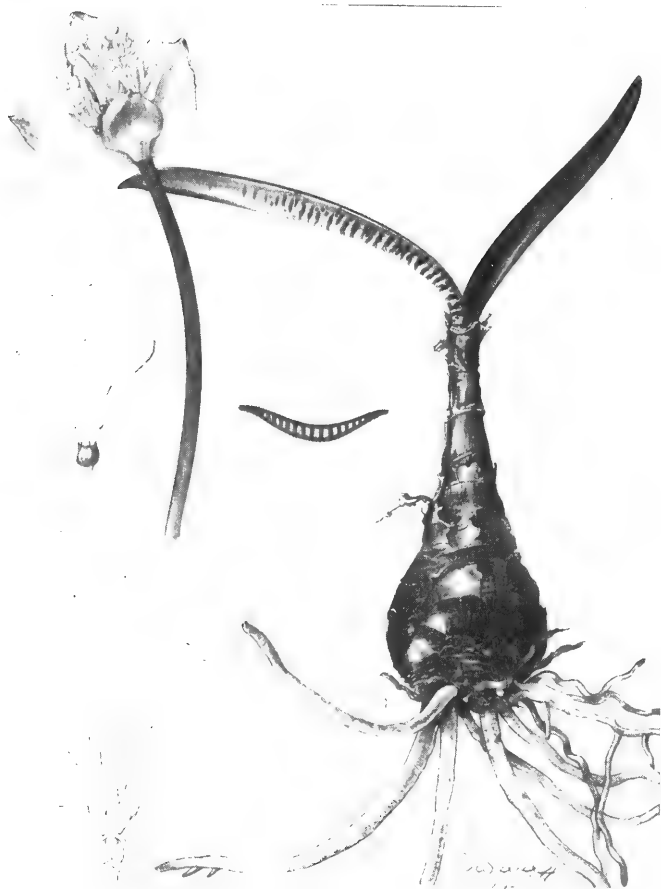


FIG. 2.

Haemanthus barkerae Snijman. 1, inflorescence $\times \frac{2}{3}$; 2, flower $\times 1\frac{1}{3}$; 3, half flower $\times 2$; 4, bulb and leaves $\times \frac{2}{3}$, and transverse section of leaf $\times 2$.

to 8 mm, pink to whitish above. *Anthers* 1.5–2 mm long when open, yellow. *Ovary* subglobose 2–3 mm diam., reddish-green. *Style* slightly exceeding the stamens. *Berry* not known.

Flowering time: February—April has been recorded from cultivated plants.
Leafing period: from May until October.

Distribution: the species occurs on the plateau between the Bokkeveld mountains near Nieuwoudtville in the west to the Hantamsberg in the east. The most northerly locality yet recorded is near to Loeriesfontein. Throughout this area *H. barkerae* is found in localised populations of several scattered individuals which grow in heavy clay soils on flat or sloping terrain (Fig. 3).

Haemanthus barkerae is distinguished from all other pink-flowered species in the genus by its leaves which are narrow, lorate and almost parallel-sided. They are somewhat canaliculate towards the base, mostly bear short stiff hairs and are characteristically barred with dark green and red on the undersurface.

In the past *H. barkerae* has been called *H. pumilio* Jacq., a name which has been loosely applied in South African herbaria to various Western Cape species of *Haemanthus*, having inflorescences with pink, spreading spathe valves. *Haemanthus pumilio* Jacq. *sensu stricto* has lorate leaves which are shorter (95–130 mm long) and narrower (5–15 mm wide) than those of *H. barkerae*; they are always glabrous and usually twisted. It is limited to the flats in the vicinity of Stellenbosch.

This attractive new species is named in honour of Miss W. F. Barker who, in addition to being the first to make a complete collection of this species, has contributed greatly to the knowledge of the genus as a whole through her meticulous collections of many other *Haemanthus* species.

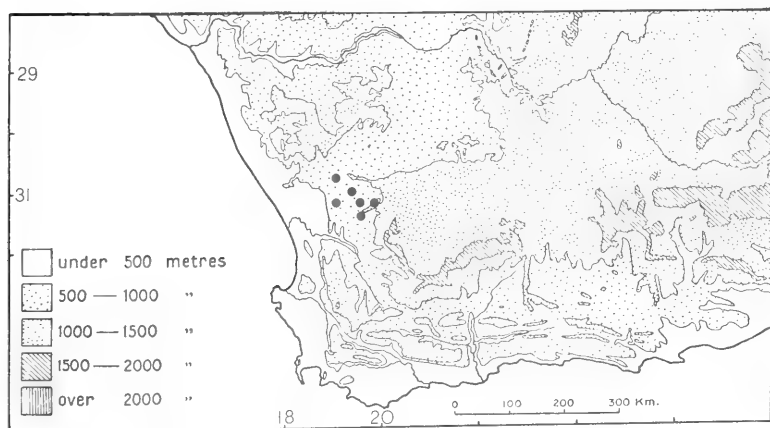


FIG. 3.
Distribution of *Haemanthus barkerae* Snijman.

CAPE—3019 (Loeriesfontein): kloof 3 miles south of Loeriesfontein (—CD), *E. Oliver s.n.* (NBG).

—3119 (Calvinia): Kokerboomkop between Loeriesfontein and Nieuwoudtville (—AB), *Hiemstra & Hardick s.n.* (NBG 899/71); farm Brandkop, 46,2 km from Loeriesfontein towards Nieuwoudtville, *Snijman 136* (NBG, PRE); 63,5 km from Calvinia towards Loeriesfontein, *Snijman 132* (NBG, PRE); farm Charleyse-Hoek, Nieuwoudtville (—AC), *Hall 4134* (NBG); farm Glen Lyon, near Nieuwoudtville, *Mauve & I. Oliver s.n.* (PRE 57721); 1,6 km from Calvinia/Loeriesfontein road towards Turon (—BC), *Snijman 130* (NBG); Akkerdam, lower slopes of Hantamsberg (—BD), *Barker 9341* (NBG); Kareeboomfontein, Calvinia, west of Rebunie (—DA), *Hanekom 2374* (PRE).

ACKNOWLEDGEMENTS

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BOOK REVIEWS

FIELD AND LABORATORY EXERCISES IN ECOLOGY, by Stephen D. Wratten and Gary L. A. Fry, with pp. 227, soft cover, 227 × 148 mm. Edward Arnold Ltd., 41 Bedford Square, London WC1B 3DQ, 1980. R17.80.

The stated aim of this book is to show how modern numerical techniques in plant and animal ecology can be used practically at school, college and undergraduate level to demonstrate many of the fundamental principles of ecology. The authors, from Southampton and Scotland respectively, have gone a long way to achieving their aim in a fairly simple, well-indexed, illustrated and referenced text. However, the examples and exercises are all from Britain and so the relevance to South African conditions is usually fairly remote. Nevertheless most of these can be readily interpreted if the teacher and/or lecturer is willing to adapt the text to local conditions.

The text is divided into five major sections which are: sampling, spatial pattern, populations, population interactions and community analysis.

I felt that the section on sampling should have had a section on the determination of minimum or optimum quadrat size. Also the line intercept method is not mentioned which is a pity. Otherwise the sampling section is adequate with both field and laboratory exercises given. The section on spatial pattern has adequate cover with exercises on the detection of pattern, scale and the detection of directional pattern. The sections on populations and population interactions is essentially animal orientated but there are exercises on survivorship curves of woodland trees and cycling variation in *Culluna vulgaris*, as well as some ideas for studying plant-animal interactions and allelopathic effects of barley on weed species. The final section on community analysis is perhaps the best section and some interesting and stimulating exercises are discussed. These include diversity, species interactions, ordination and classification. It is a pity that a brief introduction to classical phytosociological classificatory techniques is omitted from this section.

In conclusion I would recommend that all teachers of ecology should certainly consider this publication as a possible addition to their library as there is much to gain from it. However, as a basic text for our region it is not really satisfactory.

E. J. MOLL

PHYSIOLOGICAL PLANT ECOLOGY, by W. Larcher, with pp. xvii + 303, 193 figures and 47 tables. 228 × 152 mm. Berlin, Heidelberg, New York: Springer-Verlag, 1980. Soft cover, approx. US \$34.90.

This is a well-revised second edition which although it has lost some of the more detailed information of the first edition, has covered the field of physiological plant ecology extremely well. The concepts given and the examples used to illustrate them are up-to-date, and the bibliography is fairly comprehensive. To have covered the field as well as Larcher has done in this present, fairly modest volume, is certainly an achievement.

The layout of the book is good with an introductory chapter on the environment of plants followed by one on radiation and temperature. This is followed by chapters on carbon utilization and dry matter production, the utilization and cycling of mineral elements, water relations, and finally a synopsis in which there is an analysis of ecological factors and some commentary on data synthesis, ecological models and computer simulation.

Throughout the book the examples chosen are such that plants from environmental extremes have been selected to demonstrate the factor being considered. So we find the radiation load of a cactus is compared to that of an alpine plant, the seasonal variation in starch storage in deciduous trees is compared to that of evergreen trees, and the water balance of an oak with and without leaves is discussed.

As the author mentions in the preface, this book "is not intended*as—nor could it be—a comprehensive textbook of plant ecology; it is one of many possible ways of presenting what is known in the field." Although many of the examples chosen are not South African ones, the concepts considered often are and the current edition would be extremely useful as an undergraduate text for any physiological plant ecology course. The book is also an extremely useful postgraduate reference and a must for every library.

E. J. MOLL

ECOLOGY, by Hermann Remmert, with pp. viii + 289, 189 figures and 12 tables. 242 × 266 mm. Berlin, Heidelberg, New York: Springer-Verlag, 1980. Soft cover, approx. US \$29.90.

Although the author has achieved a much more functional approach to the study of ecology than many others, this is really just another ecology text by a European zoologist. This may sound unkind, but the relevance of the book to the South African situation is minimal, and it is even less applicable to the South African plant ecologist. Nevertheless the text is written in an easily readable style, and it does make interesting and stimulating reading. The examples are well chosen and the index and bibliography are adequate.

This book would be a very useful acquisition to libraries, and it may also be a useful undergraduate text for certain courses in ecology. In the main, however, this text will probably not prove very popular as there are other better suited texts in the field.

E. J. MOLL

TAXONOMIC ASPECTS OF AFRICAN ECONOMIC BOTANY: PROCEEDINGS OF THE IX PLENARY MEETING OF ASSOCIATION POUR L'ETUDE TAXONOMIQUE DE LA FLORE D'AFRIQUE TROPICALE (A.E.T.F.A.T.). Las Palmas de Gran Canaria, 18–23 March, 1978, edited by G. Kunkel, with pp. 250. Obtainable from: The Secretary, Bentham-Moxon Trust, Royal Botanic Gardens, Kew, Richmond, England TW9 3DS. Price £11. Surface postage paid.

With the tenth Plenary Meeting of A.E.T.F.A.T. planned to take place in Pretoria from 19–22 January, 1982, it is pertinent to review the Proceedings of the ninth Plenary Meeting which are contained in a cleanly attractive, clearly printed, not very strongly bound, modestly sized volume published in September, 1979.

The main theme of the ninth session was taxonomic aspects of African economic botany. Of the nearly sixty lectures presented, only nineteen contributed to this theme. The essence of these lectures is given in Part II of the Proceedings, subtitled Notes on African Economic Botany, and introduced by F. N. Hepper of the Royal Botanic Gardens, Kew.

These papers deal with families of plants (7), genera (5), species (2), or concern groups of plants with special significance to man (5—for example, edible products; water plants; coverage of mining wastes).

Most of the papers are short and while being ". . . fascinating and instructive . . ." to quote Hepper in his introduction, are essentially reviews that reflect very directly the paucity of recorded knowledge relating to the economic importance of indigenous African plants, and the extent of work awaiting the researcher in this field and in the field of

ethnobotany. The last paper in this Part is a general one by J. B. Gillett of the East African Herbarium, Nairobi. I draw attention to it in particular because it carries a significant message for the young and the potential biological scientists of the African continent by stressing the need for the recording, and thus preserving, of the tribal uses of wild plants, information very hard-won by generations of ancestral people and usually closely guarded.

Without doubt, here is an extremely worthwhile aspect of research awaiting those with biological or pharmacological interests whose background is set in, among others, the independent countries so closely related geographically to South Africa, and who, because of this advantageous association, are so especially suited to undertake this work.

Part III, subtitled Systematics, Sociology and Geography, encompasses twelve papers. The content is varied and always interesting: some are longer and more detailed than are the majority of papers of Part II. As might be expected from the subtitle, nearly all the articles deal with a particular plant group from a particular aspect. Seven are written in French.

Part IV (11 papers) comprises progress reports which record advances and proposals for advances in floristic and phytogeographic research in the flora of Africa south of the Sahara. This Part is thus in keeping with the traditions of A.E.T.F.A.T.

Part V (11 papers) covers Projects and Miscellaneous Communications. Here are set out statements of work being undertaken and methods being followed; difficulties experienced by institutions and by individual workers; an appeal, and two longer articles, the one dealing with alien plants in South Africa, the other with mimetic weeds.

Part I differs from all the other Parts. In it are reproduced the texts of three inaugural lectures presented during the Las Palmas Meeting. These lectures commemorate the life and work of C. Linnaeus (presented in French by O. Hedberg); C. P. Thunberg (B. Nordenstam); and A. P. de Candolle (J. Miegé). Each is relatively short and historically significant in the context of the taxonomic botany of the African flora. Collectively these texts make a worthy opening to a volume that should prove stimulating as a source of ideas to postgraduates commencing their careers. Established researchers will also find many aspects to hold their attention and much to provoke them yet again to the thought that in relation to assessment of the world's natural plant resources, far too little is known of the flora of Africa south of the Sahara.

The book itself is pleasing to handle, but it will not endure too much of this without showing signs of wear. In the foreword the editor refers to certain "technical hitches" which delayed publication, so the reader is conditioned to expect some possible inaccuracies in the text: but these do not obtrude. Illustrations are not numerous because a majority of the papers do not require clarification by this means. Those that are included are generally well reproduced and easily interpreted. There are comprehensive lists of references with most of the papers. No index is included and I found unusual the placing of the page of contents at the end of the volume rather than at the beginning.

K. D. GORDON-GRAY

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